SPATIO-TEMPORAL DISTRIBUTION, HABITAT USE, AND DRIFT OF EARLY LIFE STAGE NATIVE FISHES IN THE LITTLE COLORADO RIVER, GRAND CANYON, ARIZONA, 1991-1994

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Anthony T. Robinson, Robert W. Clarkson[1],
and Robert E. Forrest[2]

Arizona Game and Fish Department
2221 West Greenway Road
Phoenix, Arizona 85023

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Current address: U.S. Bureau of Reclamation, Biological Resources Branch, 23636 N. 7th St., Phoenix, AZ 85068

Current address: EcoPlan Associates, Inc., 1845 S. Dobson Rd., Suite 111, Mesa, AZ 85202

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Abstract--We investigated spatio-temporal distributions, drift, and habitat use patterns of larval humpback chub (*Gila cypha*), speckled dace (*Rhinichthys osculus*), bluehead sucker (*Pantosteus discobolus*), and flannelmouth sucker (*Catostomus latipinnis*) in the Little Colorado River (LCR), a tributary to the Colorado River in Grand Canyon, Arizona, from 1991 to 1994. Spring larval drift and near-shore distribution patterns suggested all native fishes spawned throughout 14.2 km of the LCR immediately above the mouth. There was near complete overlap in timing of the spawn among these four species. Larvae of all species were collected in the drift, and drift was greater near-shore than midchannel. More larvae drifted during night than day, and diel periodicity was evident for all species except flannelmouth sucker. We estimated that over 377,000 native fish larvae drifted out of the LCR into the Colorado River during a 46 day period in 1993. Larval trap collections suggested larvae of all four species actively moved among near-shore habitats. Logistic regression indicated a large amount of overlap in habitat use among species during base flow and high flow (flooding) conditions. Significant differences in habitat use were observed among the larval stages of all species except humpback chub. Older life stages of all species, however, showed a trend towards use of higher flow velocities, deeper water, and areas farther from shore. Behavioral observations of larvae indicated that the two cyprinids and flannelmouth sucker tended to use the upper pelagic zone more than bluehead sucker. In addition, bluehead sucker larvae increased their use of the benthic zone as they aged, while the two cyprinids and flannelmouth sucker decreased their use of the benthic zone as they aged.

Introduction

The ecology of early life stages of the native ichthyofauna of the Colorado River Basin, southwestern USA, has been little studied, with the exception of Colorado squawfish, *Ptychocheilus lucius* (Haynes et al. 1984, Tyus and McAda 1984, Tyus 1986, Karp and Tyus 1990, Tyus and Haines 1991, Stanford 1994). Early life stages are critical in the life histories of these fishes, especially under present environmental conditions. Hypolimnial-release reservoirs in the basin create tailwater temperatures unfavorable for egg (Marsh 1985) and larval development (Lupher and Clarkson 1993), and decrease larval swimming abilities (Childs and Clarkson, in prep.). In addition, a sizable array of nonindigenous predatory and competitory fishes elevate early life stage mortality rates (Minckley 1983, 1991; Dunsmoor 1993; Hendrickson 1993; Ruppert et al. 1993). Many of these native species are threatened or endangered, or are being considered for such status.

Spawning sites of most native fishes in the Colorado River Basin are typically in areas of relatively swift current (Minckley 1973, 1991; Maddux and Kepner 1988; Tyus 1991; Weiss 1993), a presumed adaptation to enhance egg oxygenation and removal of metabolic wastes (Hontela and Stacey 1990). However, because larvae have difficulty contending with swift currents (Harvey 1987, Childs and Clarkson, in prep.), and swift water areas are poor producers of zooplankton (a major food source for many larval fishes) (Hynes 1970, Minckley 1973, Maddux et al. 1987, Snyder 1990, Clarkson and Robinson 1993), larvae may disperse from hatching sites to other areas to satisfy their energy requirements (Corbett and Powles 1986, Tyus and Haines 1991). Transport of larvae from hatching sites via drift or active movement may be of major significance in the ecology of Colorado River Basin native fishes (Tyus and McAda 1984, Tyus 1986, Tyus and Haines 1991, Stanford 1994).

Three of the eight fish species native to the Grand Canyon area of the Colorado River in Arizona are extirpated (Colorado squawfish; bonytail, *Gila elegans*; roundtail chub, *G. robusta*), and one is extremely rare (razorback sucker, *Xyrauchen texanus*). The four extant native species (humpback chub, *G. cypha*; flannelmouth sucker, *Catostomus latipinnis*; bluehead sucker, *Pantosteus discobolus*; and speckled dace, *Rhinichthys osculus*) are known to spawn and rear in the Little Colorado River (LCR), a major tributary entering the Colorado River in Grand Canyon. However, precise spawning locations of species in the LCR have not been determined. If spawning sites are localized longitudinally, the temporal and spatial distribution of larvae in near-shore habitats immediately following spawning may identify major spawning reaches. If there is fidelity to spawning sites across years, such locality information could be used to more precisely define sites of egg deposition for future studies of reproduction. One objective of our study was to determine spatio-temporal distributions of larvae in near-shore habitats in the LCR.

Techniques that monitor movements of fishes among near-shore habitats can provide further insight into larval dispersal mechanisms (Brown and Armstrong 1985, Harvey 1991). A second objective of our study was to determine drift patterns of native fish larvae, and to determine if larvae move among near-shore habitats. The extent of native fish drift from the LCR to the Colorado River was also estimated.

It is unknown on what basis larvae populate suitable rearing habitats once they have moved from hatching sites. Since larval movements are limited by current velocities, hydraulic variables may dictate whether a given habitat is accessible from the mainstem (Floyd et al. 1984; Harvey 1987, 1991). Algal, zooplankton or invertebrate densities, substrate types, cover attributes, presence of predators, or physical-chemical variables may ultimately determine suitability of accessible habitats. Our third objective was to describe near-shore habitats used by larval native fishes in the LCR.

A fourth objective was to describe the behaviors of the little studied larval and juvenile native fishes in the LCR. Species, and age-classes within species, may behaviorally segregate among and within habitats. For instance, several species may be present in the same habitat, but forage or use the water column differently. Knowledge of species behaviors such as foraging, schooling, agonistic interactions, etc., will fill life history gaps and thus be useful for conservation purposes.

Study Area

Our study was conducted in the lower 14.2 km of the LCR in Grand Canyon, Coconino County, Arizona. The upper boundary is Chute Falls, a landmark delimiting the distrubtions of the three large-bodied native fishes (humpback chub, bluehead sucker, and flannelmouth sucker) (Figure 1). Speckled dace is present both above and below the falls.

Perennial waters of the LCR in the study area originate from Blue Spring (21 km) and a downstream series of springs that typically provide 6.31 m^3/s of flow at the mouth (Johnson and Sanderson 1968, Cooley 1976). Waters of these springs are 20°C, salty, highly charged with free carbon dioxide, and oversaturated with calcium carbonate (calcite; Cole 1975). As the waters flow downstream from Blue Spring, carbon dioxide vaporizes and calcite precipitates. This process is most noticeable below a series of large tufaceous dams known as the Atomizer Falls Complex. Chute Falls is the uppermost dam of this series.

At base flow the river below Atomizer Falls Complex is characterized by a milky blue color, substrate largely covered with white, uncemented calcite particles, and numerous tufaceous limestone formations, all results of calcite precipitate. From Chute Falls to Big Canyon (11.5 km), fine-grained substrates predominate, although boulder-dominated rapids and tufaceous dams also occur. Below Big Canyon substrates consist of fewer tufaceous formations and more boulders. Near-shore low velocity (<0.2 m/s) habitats vary from unvegetated and vegetated (e.g. *Typha*, *Scirpus*, or *Phragmites*) shoreline margins with mostly fine-grained stubstrates to shallow, boulder-dominated shoreline invaginations. Midchannel bars and islands with associated slow current velocities are relatively rare.

The LCR exhibits wide flow fluctuations (Figure 2) as a result of runoff from winter snowmelt and summer convective storms. For example, the reach above Blue Spring varies temporally between dryness and large scale floods; a flood of 2830 m^3/s was estimated on September 19, 1923 (U. S. Geological Survey 1954). As a result of fluctuating flow and solar irradiation, the LCR also exhibits large seasonal fluctuations in temperature (Figure 3). However, because of stenothermal spring inputs, temperature extremes are ameliorated.

Methods

Flow data reported in our study were obtained from the USGS gauging station near Cameron, AZ (ca. 65 km above Blue Spring). Input to the LCR below Cameron is ungauged, but we considered zero flows near Cameron (indicating no runoff in the ephemeral portion of the river above Blue Spring) to represent base flow from the perennial springs.

Larval Fish Distributions and Reproductive Activity

We quantified the temporal appearance and spatial distributions of larval native fishes in the LCR by surveying near-shore low velocity habitats (current velocity < 0.2 m/s and bounded on at least one side by shoreline) in the study area during spring-summer, 1992-1994. Shorelines (both banks) were surveyed once or twice weekly, and presence or absence of larval fishes in contiguous 100 m reaches was recorded. At base flow, near-shore waters were shallow and clear enough to allow direct observation of small fishes. During turbid conditions, we sampled with fine-meshed dip nets and seines.

Larval collections were made in 100 m reaches at 0.5 km intervals to avoid oversampling, unless absence of larvae in those reaches required collections from adjacent areas. When possible, fish were identified to species in the field; if not, specimens were preserved (10% formalin or 95% ethanol) and identified in the laboratory. Total length (TL, ± 1 mm) of larvae was measured, and larvae were assigned to one of three ontogenetic groups (Snyder 1981, Snyder and Muth 1990): 1) protolarvae (undeveloped spines or rays associated with future median fins); 2) mesolarvae (morphogenesis of distinct principle rays in the median fins); and 3) metalarvae (presence of full adult compliment of principle fin rays in the median fins and presence of pelvic fins or fin buds). Our larval stage length frequency data generally conformed with data presented by Snyder (1981) and Snyder and Muth (1990). We therefore assigned each fish to a larval stage based on its length, using Snyder's length categories.

Day of spawning (D_s) of humpback chub was estimated by a formula similar to Haynes' et al. (1984):

$$D_s = D_c - \left(\frac{L_c - L_o}{G} + P \right)$$

where P = a 5 d egg incubation period (Marsh 1985), L_o = 7 mm hatching length (TL) (Snyder 1981), L_c = length (TL) of collected larvae, D_c = collection day, and G = a growth rate of 0.26 mm/d at 20°C (Lupher and Clarkson 1993). Most larvae in the LCR were captured during base flow when water temperatures were near 20°C (Figure 3). Using peak hatching time (6.5 days) at 15°C (Marsh 1985) would result in estimated dates only 1-2 d earlier in the year. We did not estimate spawning dates for the other three native fish species, since not all of the parameters necessary for the calculations are known.

Larval Fish Movements

We collected larval fish drift samples from two sites in the LCR (10.5 and 1.9 km above mouth) from May 1991 to July 1993. Drift nets were deployed for 24 h during the first week of each month, except during May and June when they were deployed for 24 h twice weekly. During May 1991, nets were set opportunely throughout the day. During June-November 1991, nets were set at 12 h intervals. For the remainder of the study, nets were set at 6 h intervals at 0000, 0600, 1200, and 1800 h. Net fishing time was dependent upon flow conditions: 6 h at base flow, but as brief as 1 min during periods of high runoff. Drift was collected in nets (0.5 m x 0.5 m opening; 3 m long; 750 μm mesh) fitted with removable collection buckets containing a 500 μm mesh screen. At water depths <0.5 m, nets were set just above the river bottom; at depths >0.5 m, nets were set just below the surface of the water. At each site, three drift nets were positioned across the river, one within 1.5 m from each shoreline and one midchannel.

Current velocity at the drift net entrance was measured with a Marsh-McBirney model 201D electromagnetic velocity meter. Contents of each net were rinsed into jars, preserved with 10% formalin, and returned to the laboratory for analysis. All fishes were identified, enumerated, and assigned to a developmental phase according to Snyder (1981) and Snyder and Muth (1990). Fish eggs were enumerated, but not identified to species.

Drift densities were computed as numbers of larvae or eggs per 1,000 m^3. We used the nonparametric Kruskal-Wallis one-way anova (K-W) (Zar 1984) to assess temporal and spatial variation in ranked densities. For diel periodicity, only samples in which set times and durations fit into four time periods (0000-0559, 0600-1159, 1200-1759, and 1800-2359 h) were analyzed.

A third site (300 m above mouth) was also sampled May-June 1993 in an attempt to estimate the numbers of fishes and eggs that drifted out of the LCR. Six drift nets were positioned at equidistant sites across the river. Nets were deployed twice weekly for a 24 h period, and were run at 12 h intervals. Total numbers of fishes drifting into the mainstem per 24 h period were estimated by calculating number of fish per volume of water filtered for all six nets and extrapolating to the number at 546,973 m^3 of water (approximate output at the mouth of the LCR per 24 h at a base flow of 6.31 m^3/s). These daily totals were plotted, and total area under the curve was calculated using the trapezoidal rule to estimate total numbers of fish that drifted out of the LCR in May and June of 1993.

A pilot study was conducted in 1993 to determine if larval traps were effective to investigate directional dispersal of larval fishes in near-shore habitats. Three larval traps were placed in each selected occupied and unoccupied peripheral pool or shoreline margin habitat; one at the point of inflow (facing upstream), and two at the point of outflow (one facing upstream and the other facing downstream). Traps were similar to the design of Culp and Glozier (1989), and were made from transparent plastic 500-1000 ml wide-mouth bottles, with the central portion of the bottom and screw cap cut out. Jars were fitted with a 500 μm-mesh stainless steel screen funnel in the cap and a flat screen on the bottom. Traps were deployed May through August, and were run twice weekly at 6-h intervals for a 24-h period. Data were statistically analyzed with the K-W test.

Habitat Use

In 1993 we measured the following habitat variables at fish collection sites: depth, current velocity, substrate, distance from shore, and habitat cover features. Measurements were taken during base and high flow conditions in near-shore larval and young-of-year (YOY) habitat within the lower 100 m of each 500 m reach. High flows during habitat use measurements ranged from 0.28-1.98 m^3/s as measured at the gauge near Cameron. Measurements were recorded at points along one to three perpendicular-to-flow transects. These transects were spaced evenly, at least 10 cm apart, and extended through the area in which fish were collected. Number of transects sampled depended on the size of the area inhabited by fish: if the area was <10 cm wide, one transect was established; if the area was 10-20 cm wide, two transects were established; and if the area was >20 cm wide, three transects were established. Depth was measured to $\pm$ 1 cm, current velocity to $\pm$ 0.1 m/s using a Model 201D Marsh-McBirney electromagnetic flow meter (if depth $\geq$ 5 cm) or beads of neutral buoyancy drifted and timed over a distance of 10 cm (if depth $<$ 5 cm), distance from shore to $\pm$ 1 cm, and substrate and habitat cover features according to criteria in Table 1. We used the mean value of each variable (except cover) from each collection site for data analysis.

Fish collection, measurement and classification methods were those detailed above under the larval fish distributions and reproductive activity section. We tested for ontogenetic habitat shifts among larval stages, and all fish $\leq$30 mm were included in among-species comparisons of habitat use (due to large differences in maximum size of larvae among species).

All habitat use variables had nonnormal distributions, unequal variance-covariance matrices, and could not be transformed to normality. We therefore used forward stepwise logistic regression to describe the multivariate habitat use of YOY native fish $\leq$30 mm in the LCR (Hanusheck and Jackson 1977, Press and Wilson 1978). This procedure allowed for simultaneous analysis of categorical and continuous data. None of the variables included in our analyses were correlated ≥ 0.2 with other variables used in the equations. Variables were removed from the model using the likelihood ratio test (SPSS 1992) with a significance level of 0.05. The variable "feature" was coded in the logistic model as a categorical variable indicating presence ("-1") or absence ("+1") of cover, rather than including all categories shown in Table 1. We did this because cover features were frequently absent at our collection localities.

In our logistic regression models, "habitat use" data only consists of habitats used by YOY fish ≤30 mm. Thus, we define "absence" (or more appropriately "unused" habitat) as all data points used by fishes other than the target species. Following this categorization, we took a random subsample of data from the "unused" category equal in size to the "used" category to enhance the predictive ability of the logistic model. This use of the logistic model therefore reflects overlap in habitat use among native fishes in the LCR. A model equation with high predictability of presence or absence of a particular species would indicate that a species used habitat in a different way than others. Low predictability would indicate overlap in habitat use with other fish species.

The K-W test was used to investigate differences in habitat use among species and larval stages of each species. Non-parametric multiple comparisons (Zar 1984) were used to separate significant differences in habitat use among species and larval stages. We compared use of cover features among species with Kendall's rank concordance test (Sokal and Rohlf 1981). This test was also used to examine trends in mean ranks of each larval stage, among species, for all other habitat variables.

Young-of-Year Behavior

YOY native fishes in near-shore habitats were observed using time bound focal animal behavioral techniques (Altman 1974) to characterize species and species size class activities (general behaviors and vertical positions in the water column). During clear-water conditions in 1991-1994, individuals of selected length categories (≤30, 31-50, and 51-100 mm) were randomly selected and observed for 5 min. Behaviors were recorded on audio tape according to the following mutually exclusive categories: feeding (on bottom, on plants, in the water column, at the surface), and nonfeeding (swimming; schooling; chasing; being chased; other, such as resting, hiding, etc.). Cumulative time spent in each category was transcribed from the tape recordings. When fish could not be identified to species visually, they were collected and identified following observations.

At the initiation of each behavior, vertical location of the fish in the water column was recorded within five zones: (1) benthic = in contact with the bottom; (2) lower pelagic = lower one-third of water column, but not in contact with bottom; (3) mid-pelagic = middle one-third of water column; (4) upper-pelagic = upper one-third of water column but not at surface, and; (5) surface = at surface. Fish were observed during early morning, mid-day, and late afternoon.

Differences in percent time exhibiting each behavior among species and length categories within species were analyzed with the K-W test. Frequencies of vertical zone observations were converted to percentages and analyzed with K-W tests, and non-parametric multiple comparisons (Zar 1984).

Results

Larval Fish Distributions and Reproductive Activity

Thirty-one longitudinal larval fish surveys were completed: 12 in April-September, 1992; 11 in April-August, 1993; and 8 in March-June, 1994. No obvious longitudinal distributional patterns were detected either within or among surveys or years for native fish protolarvae (Figure 4 and Appendix I a, b and e), and no specific spawning locations were suggested. Speckled dace protolarvae were collected throughout km 0-14.1 during longitudinal surveys, and as far upstream as Blue Spring (21.0 km) during opportunistic sampling. Humpback chub and bluehead sucker protolarvae were collected upstream to 13.5 km, and flannelmouth sucker protolarvae were collected upstream to 13.0 km. In general, protolarvae were captured less frequently than mesolarvae for all species (Table 2).

Both mesolarvae and metalarvae of all native species were widely distributed in near-shore low velocity habitats throughout the lower 14.2 km of the river (Appendix I c, d, f and g). Compared with mesolarvae, we found metalarvae of the two catostomids in relatively few near-shore habitats during surveys. In contrast, humpback chub (1993 and 1994) and speckled dace metalarvae were more widely distributed than their mesolarval stage (Appendix I c, d, f and g). In 1992, humpback chub mesolarvae were observed more frequently than metalarvae (Appendix I a).

Based on back-calculations from larval lengths, humpback chub spawning began in March in 1991-1993, and likely peaked during April of each year (Figure 5): 70% of the estimations occurred in April in 1991, 80% in April in 1992, and 63% in April in 1993. Also in 1991-1993, most spawning was completed by the end of May; however, sporadic spawning likely occurred in June in 1991 and 1993, and into July in 1992. In 1994, the majority of spawning occurred in

March (52%) and April (45%). However, our 1994 estimates also indicate that sporadic spawning occurred at low levels in January and February. In 1994, sampling stopped at the end of June, so estimates of June and July spawning were not possible. Overall, our estimates indicate most spawning followed peak spring runoff: 86% in 1991; 96% in 1992; 95% in 1993; and 66% in 1994. The peak spring runoff in 1993 was on March 22, although much higher flows were recorded during the January and February floods.

Larval Fish Movements

We collected 1,454 drift samples during the study: 31% contained larval fish, and 26% contained eggs. Eighty-one percent of larval fish collected were natives (38% speckled dace, 20% humpback chub, 18% bluehead sucker, and 5% flannelmouth sucker), 9% were nonnatives (4% fathead minnows, *Pimephales promelas*; 3% channel catfish, *Ictalurus punctatus*; 2% common carp, *Cyprinus carpio*), and 10% were too damaged to identify. For native species, protolarvae and mesolarvae tended to dominate collections from the drift (Table 3).

Larvae of all species drifted primarily from May through July of each year (Table 4); no larvae were found in drift samples during January-March of 1992 or 1993. Sampling in 1993 ended in July. Egg densities also peaked in the spring, although eggs were collected in every month except March and September (Table 4). Eggs in drift were generally most abundant during the last phase of spring runoff, while larval fish drift was greatest following spring runoff (Appendix II).

Overall, larvae drifted at significantly greater densities during the night (K-W $H=12.14$, $p<0.01$), but diel periodicity was not evident for all species (Table 5). Three native species (humpback chub, speckled dace, and bluehead sucker), and one nonnative (channel catfish) exhibited diel periodicity (Table 5). No periodicity was evident for egg drift.

In total, native fish larvae were more abundant near-shore than in midchannel drifts ($H=44.85$, $p<0.001$). However, this trend was not apparent for nonnative species (Table 6). Eggs were more abundant in midchannel drift, and were more abundant in drift at 1.9 km than at 10.5 km above the mouth (Table 6). Most larval fishes were more abundant in drift at 1.9 km than at 10.5 km ($H=23.90$, $p<0.001$), but humpback chub drifted at significantly greater densities at 10.5 km (Table 6).

Based on drift collected at the confluence site, we estimated that approximately 377,115 fishes drifted from the LCR to the Colorado River during May 11-June 26, 1993 (Figure 6). Eighty-one percent of these fish were native and 19% nonnative.

Larval fish were captured in traps equally among all three trap orientations ($N=2171$, $H=1.52$, $p=0.467$). Larvae of different stages were captured with equal frequencies, indicating all larval stages actively move into and out of near-shore slack-water habitats. Larvae were caught in traps more frequently at 0600-1200 h than during the other three diel periods ($H=43.53$, $p<0.05$).

Habitat Use

In 1993, a total of 10,004 habitat measurements were recorded in the LCR during longitudinal habitat surveys, representing the habitat use of 1,377 larval and YOY fish ≤30 mm (462 bluehead sucker, 129 flannelmouth sucker, 258 humpback chub, and 528 speckled dace). Two additional YOY species (common carp and fathead minnow) were found in low numbers, and they were not included in analyses. We included only five ordinal substrate categories in our analyses: boulder, cobble, sand, silt, and calcium carbonate flock. Substrate categories used ≤ 0.6% of the time were dropped from the analyses so that mean ranks of substrate data would accurately reflect substrate size used by fishes.

None of the logistic regression model equations were able to distinguish habitat use of any one species from the other three at base flow at better than 61.7% probability (Table 7). The base flow models indicate that, relative to other species, bluehead sucker YOY used shallower water, humpback chub YOY used lower flow velocities, deeper water, and larger substrates, and speckled dace YOY used higher flow velocities and were less likely to be found near cover. A significant logistic model could not be constructed for YOY flannelmouth sucker.

Habitat use differences among species were even more difficult to distinguish at high flow (Table 7). The only significant logistic model at high flow indicates that, relative to other species, YOY speckled dace used shallower water. A significant logistic model could not be constructed for YOY bluehead sucker, flannelmouth sucker, or humpback chub at high flow.

Univariate tests (Kruskal-Wallis ANOVA, SPSS 1992) for differences in habitat use among YOY species (Table 8) and subsequent non-parametric multiple comparison tests (Zar 1984, Table 9) generally conformed with the description of habitat use produced by logistic regression, indicating high overlap in habitat use among species. Similarly, use of dominant cover categories (Table 10) was concordant among species at both base and high flows (Kendall's $W = 0.907$ and 0.885, respectively; $0.001 < P < 0.005$).

Relative frequency histograms of near-shore habitat used by larval fishes and YOY ≤30 mm at base and high flow are presented in Appendix III. All species, except humpback chub, changed their habitat use with changes in larval stage (Table 11). Non-parametric multiple comparisons (Zar 1984) for separating significant differences in these tests revealed consistent patterns of change in habitat use (Table 12 and Appendix III). Base flow comparisons indicated that older lifestages of bluehead suckers used significantly higher flow velocities, older lifestages of all species except humpback chub used deeper water, and older lifestages of bluehead sucker used habitats farther from shore. Metalarval bluehead sucker used larger substrates than mesolarvae. Finally, mean ranks of flow, depth, and distance from shore for each larval stage were significantly concordant across all species at base flow (Sokal and Rohlf 1981; Kendall's W = 0.81, 1.0, and 0.81, respectively for each variable; $P < 0.05$). Mean ranks of substrate size used by each larval stage were not concordant across species (Kendall's $W = 0.19$; $P > 0.10$).

Comparisons at high flow indicated that older lifestages of speckled dace used deeper water, mesolarval bluehead sucker used areas farther from shore than protolarvae, and speckled dace metalarvae used larger substrates than did mesolarvae of that species (Table 12). Mean ranks of each variable for each larval stage were not significantly concordant across species at high flow (Kendall's $W \leq 0.44$, $P > 0.10$ for all tests).

Young-Of-Year Behavior

All four native fish species changed feeding and nonfeeding activities with size (Table 13). Small humpback chub, speckled dace, and flannelmouth sucker were more frequently benthic feeders than larger conspecifics. In addition, smaller speckled dace spent less time feeding on plants and at the water surface than larger dace. There was a significant difference in percent time spent feeding versus age for bluehead sucker, but no differences between specific feeding behaviors.

Humpback chub spent more time swimming as they grew, whereas speckled dace and bluehead sucker generally spent less time swimming with increasing size. Small bluehead sucker and humpback chub were chased by other fish more often than larger bluehead sucker and humpback chub. Flannelmouth sucker increased schooling activities as they grew. Speckled dace and bluehead sucker increased "other" behaviors as they grew (Table 13).

Vertical use of the water column changed with size (Figure 7). Compared to humpback chub >30 mm TL, chub ≤30 mm utilized the bottom more (K-W $H=7.42$, $p<0.05$) and the mid-pelagic zone less ($H=19.55$, $p<0.05$). Humpback chub ($H=7.21$, $p<0.05$) and speckled dace ($H=8.92$, $p<0.05$) 31-50 mm utilized the surface more than those in the other two size classes. In addition, larger speckled dace utilized the mid-pelagic zone more than smaller conspecifics

($H=6.64$, $p<0.05$). For the catostomids, bluehead sucker utilized the lower pelagic zone less with larger size ($H=7.19$, $p<0.05$). Flannelmouth sucker decreased utilization of the bottom ($H=5.87$, $p<0.05$), and increased use of the upper pelagic zone ($H=9.97$, $p<0.05$) with increasing length.

Discussion

We believe the four extant native fish species spawn throughout the LCR below Chute Falls (14.2 km), since proto- and mesolarvae were found scattered throughout this reach. However, humpback chub larvae were more abundant in the drift at 10.5 km than at 1.9 km, suggesting spawning for this species may be concentrated at or above 10.5 km. Although specific spawning sites may be present, we were unable to detect them. Like Colorado squawfish (Haynes et al. 1984, Tyus and McAda 1984, Tyus and Haines 1991), larvae of the native fishes in the LCR may drift long distances, and thus quickly may become widely scattered throughout the river.

Both our longitudinal survey data and our drift data suggest a March-June spawning period, peaking in April, for native fishes in the LCR, as also reported by others (Kaeding and Zimmerman 1983, Tyus and Karp 1990, Minckley 1991). The two catostomids and humpback chub also spawned sporadically at low levels in the fall and winter. Based on collections of larvae, speckled dace spawned during most periods of the year, likely in constant temperature spring outflows.

The peak in egg densities during the last phase of spring runoff and peaks of larvae during periods of base flow following runoff suggests decreasing flows may cue spawning, as has been suggested for Colorado squawfish (Tyus 1986, Nesler et al. 1988). Tyus (1990) suggested temperature and photoperiod are also important spawning cues.

The paucity of larval fish captured during May 1992 longitudinal surveys compared to May 1991, 1993, and 1994 may be partly attributable to less efficient sampling caused by high flows and turbidity in 1992. However, we believe it was more likely due to a scarcity of larvae. After the May-June 1992 flooding events, few larvae were observed, indicating floods may have killed larvae or flushed them from the river. Flooding during the spawning season may have a negative effect on spawning success (Seegrist and Gard 1972, Harvey 1987), killing eggs and larvae. Næsje et al. (1986) found a concurrent increase in cisco and whitefish larval drift with an increase in flow. Habitat availability measurements during high flow events showed less near-shore, slow velocity habitat was available than during base flow events (AGFD unpublished data). Combined with higher turbidity of elevated flows and a likely diminution in the density of invertebrate food items, starvation may have also contributed to fewer larval fish in 1992.

The propensity of protolarval humpback chub and speckled dace to drift, but to be relatively uncommon compared to other larval stages in near-shore slack-water habitats, suggests they are poor swimmers and are largely at the mercy of the current. As humpback chub and speckled dace developed into meso- and metalarvae, fewer drifted, but more were observed in near-shore habitats. Mesolarval and metalarval distributions may be more reflective of habitat preferences than of adult spawning sites. In addition, larval trap catches indicated that larval movement into and out of these near-shore habitats is not completely passive. Fish of all four native species were captured in downstream facing traps, suggesting larvae actively disperse into near-shore habitats. We have no data to indicate whether such movements are density dependent or density independent. Larvae of all four species were also captured in upstream facing, pool outflow traps indicating larvae moved out of near-shore habitats.

The propensity for larvae to drift near-shore is likely a result of the abundance of larvae in near-shore habitats, as well as movements of these fishes into and out of these habitats. Pavlov et al. (1978), Brown and Armstrong (1985), and Valdez et al. (1985) also reported greater larval fish drift densities near-shore than midchannel, and Pavlov et al. (1978) suggested this difference was a behavioral response. Brown and Armstrong (1985) suggested greater near-shore drift densities of larval fish were due to hydraulic effects and habitat preferences of larvae.

A somewhat different drift pattern was evident for native catostomid larvae. Protolarvae of both species were common in the drift as well as in near-shore habitats, suggesting they may actively move into and out of near-shore habitats and drift in search of suitable habitat. Scarcity of sucker metalarvae in near-shore habitats and drift suggests an ability to avoid drifting. As suckers aged they used habitats further from shore, thus they were rarer in our collections.

Our results showed native fishes, other than flannelmouth sucker, were prone to drift at night. Of nonnative fishes, only channel catfish exhibited diel periodicity, drifting more at night. The tendency for larval fish to drift at night may result from negative phototaxis (Woodhead 1957, Geen et al. 1966), visual disorientation at night and accidental entry into the drift (Hoar 1953, Northcote 1962, Lindsey and Northcote 1963, Bardonnet 1993), nocturnal feeding habits (Müller 1978), or predator avoidance (Gale and Mohr 1978, Clark and Pearson 1980, Armstrong and Brown 1983). We believe disorientation is the most plausible explanation for diel drift patterns in our study. If nocturnal drift is an avoidance response to visual predators, or a result of negative phototaxis, then larvae would not be expected to drift during the day. We detected significant daytime drift of larvae of all species except channel catfish. In addition, native fish larvae in our study drifted primarily near-shore, where shallower waters would allow more accurate visual orientation. Food resources may also be more readily available in near-shore habitats.

Low predictive ability of the logistic regression models indicates that YOY (≤ 30 mm) bluehead and flannelmouth sucker, humpback chub, and speckled dace, overlapped extensively in their use of measured near-shore habitat variables under both base flow and high flow conditions in the LCR during 1993. The logistic models do provide some insight into how species, relative to one another, used multivariate habitats, but we stress that observed differences were minor, and that overall there was high overlap among species. Concordant use of cover by all four YOY native species supports this conclusion. Our behavioral observations also indicated high overlap among species; YOY (≤ 30 mm) of all species foraged off the bottom more than from the water column or off plants, and were observed near the bottom more than any of the other vertical water column categories. High overlap in habitat use has been reported for YOY Colorado squawfish and a variety of introduced and native fishes in the Upper Colorado River Basin (McAda and Tyus 1984; McAda and Kaeding 1989).

Expectations for some family-level habitat specialization among larval fishes in free-flowing rivers (Scheidegger and Bain 1995) may not apply to the relatively unstable environment of the LCR. In this respect, the LCR is similar to the South Canadian River, Oklahoma, where overlap in habitat use among adults of several species have been attributed primarily to physical and chemical limiting factors (Matthews and Hill 1980). Hydraulic factors may dictate which habitats are accessible to larval fishes (Floyd et al. 1984; Harvey 1987, 1991), and thus restrict larval fishes from developing extensive habitat specializations.

Characteristics of near-shore areas used by YOY fishes in the LCR are quite similar to the preferred nursery habitats of a wide variety of larval freshwater stream fish (Scheidegger and Bain 1995). High overlap in near-shore habitat use among larval fish species in the LCR provides little evidence for strong interspecific competition (Moyle and Baltz 1985), and might reflect the shared use of abundant resources (McAda and Tyus 1984). If competition is minimal, overlap in habitat use could be due to the ability of channel margins to support high numbers of larvae (Leslie and Timmins 1991; Penaz et al. 1992). Benthic and planktonic food densities are greater in many of the low velocity, "backwater" habitats in the Colorado River (Grabowski and Hiebert 1989; Hoffnagle et al. 1994). Use of similar areas in the LCR by YOY fishes may be a response to greater food availability and lower energetic expenditure.

Predator avoidance (Fraser and Emmons 1984; Power et al. 1985; Schlosser 1987, 1988; Harvey 1991) is another possible explanation for overlap in near-shore habitat use, as these fishes evolved in the presence of piscivorous Colorado squawfish, now extirpated from the Lower Colorado River Basin (Minckley 1973; Moyle 1976). Although it is unknown whether Colorado squawfish were ever abundant in Grand Canyon, the four extant native species in the LCR still co-occur with Colorado squawfish in the Upper Colorado River Basin. At least one study on humpback chub (Kaeding and Zimmerman 1983) indicates that adults of this species are piscivorous as well.

We found some evidence for ontogenetic shifts in near-shore habitat use. Consistent trends (concordance of mean ranks) in habitat use among larval stages indicates that, at base flow, older lifestages of larval fish used higher flow velocities, deeper water, and areas farther from shore. This pattern of habitat use is common among salmonid YOY (Lister and Genoe 1970; Everest and Chapman 1972; Symons and Heland 1978) and is often related to tradeoffs between foraging efficiency and predation risk among YOY and adults of many warmwater species (Mittelbach 1981; Cerri and Frazer 1983; Werner et al. 1983a, b; Power 1984; Schlosser 1987). Habitat shifts among larval stages, however, likely reflect morphological (Snyder 1981; Snyder and Muth 1990), and related dietary (Muth and Snyder 1995) changes, rather than tradeoffs between foraging and predation.

No ontogenetic habitat use trends were detected across species at high flow. The few significant changes observed among larval stages within species, were consistent with patterns observed at base flow.

Currently native fishes far outnumber nonnatives in the LCR, indicating the importance of this river for Grand Canyon native fishes. The LCR is a large, warmwater tributary of the Colorado River where the unmodified, lower 21 km reach still exhibits seasonal flow and temperature patterns, important patterns in the evolutionary history of the native fishes. The LCR is the only productive spawning location for humpback chub in Grand Canyon. Flannelmouth sucker, bluehead sucker and speckled dace also successfully reproduce in the LCR. The LCR also provides suitable rearing habitat for these native fishes where recruitment of young into the adult populations occurs.

Our studies indicate that near-shore low velocity habitats are important nursery areas for larval fishes in the LCR. Larval fishes transported out of the LCR into the mainstem Colorado River likely seek out these types of habitat. However, due to colder mainstem water temperatures (averaging 9°C cooler than the mouth of the LCR, Kaeding and Zimmerman 1983), larval swimming ability may decrease (Childs and Clarkson, in prep.), and thus larvae may have difficulty reaching these near-shore habitats. In addition, larvae may experience thermal shock, and either die or become too lethargic (Lupher and Clarkson 1993) to effectively avoid predation or the extreme turbulence of rapids.

Further, larvae that reach near-shore habitats in the Colorado River mainstem may be repeatedly flushed out due to daily fluctuations in discharge from Glen Canyon Dam. Therefore, although large numbers of larvae typically are transported out of the LCR into the mainstem each year, we believe that few survive. Modification of Glen Canyon Dam operations to steady flows would likely stabilize and warm near-shore habitats in spring and summer, possibly enhancing survival of larval native fishes in the Colorado River.

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TABLE 1. Substrate and cover categories. Substrate categories (other than bedrock, travertine, calcium carbonate floc, and detritus) are based on criteria of Lane (1947).

Category	Substrate	Cover
1	Bedrock	Boulder
2	Travertine	Depth > 0.5 m
3	Boulder	Instream Vegetation
4	Cobble	Ledge
5	Pebble	Overhanging Vegetation
6	Gravel	Travertine Dam
7	Sand	Turbidity
8	Silt	Undercut Bank
9	Clay	Woody Debris
10	Calcium carb. Floc	
11	Detritus	

TABLE 2. Relative abundances (%) of larval stage by species during longitudinal surveys, Little Colorado River, 1992-1994. N = total collected each year.

	Humpback Chub	Speckled Dace	Bluehead Sucker	Flannelmouth Sucker
1992				
N	54	31	20	2
Proto-	5.6	6.5	40.0	0.0
Meso-	81.5	6.5	60.0	100.0
Meta-	13.0	87.1	0.0	0.0
1993				
N	318	401	614	162
Proto-	12.9	5.2	42.0	30.2
Meso-	31.8	20.0	47.9	61.1
Meta-	55.3	74.8	10.1	8.6
1994				
N	1039	615	1194	37
Proto-	1.2	1.6	24.1	5.4
Meso-	32.1	40.5	72.8	89.2
Meta-	66.8	57.9	3.1	5.4

TABLE 3. Relative abundances (%) of larval stages by species collected with drift nets, Little Colorado River, 1991-1993. N = number of fish captured.

	Humpback Chub	Speckled Dace	Bluehead Sucker	Flannelmouth Sucker
1991				
N	(11)	(304)	(21)	(30)
Proto-	54.5	85.5	52.4	30.0
Meso-	27.3	14.1	9.5	63.3
Meta-	18.2	0.3	38.1	6.7
1992				
N	(6)	(1)	(5)	(1)
Proto-	66.7	0.0	80.0	100.0
Meso-	33.3	0.0	20.0	0.0
Meta-	0.0	100.0	0.0	0.0
1993				
N	(810)	(5556)	(564)	(96)
Proto-	53.1	52.9	40.4	49.0
Meso-	40.1	46.4	53.9	39.6
Meta-	6.2	0.7	5.7	11.5

TABLE 4. Monthly mean drift densities (numbers/1000 m^3) of eggs and fish larvae, Little Colorado River. The number of drift samples in which eggs or larvae were found is indicated in parentheses. Dashes indicate samples were not taken.

1991									
Category	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Total number of samples	--	39	106	11	11	1	19	6	16
Eggs	--	8.28 (11)	2.71 (37)	0	0.04 (1)	0	0.85 (8)	0.19 (2)	0.33 (2)
Humpback chub	--	0	0.51 (12)	0	0	0	0	0	0
Speckled dace	--	0.01 (1)	0.35 (9)	15.02 (4)	0.44 (1)	0	0	0	0
Bluehead sucker	--	0	0.42 (9)	0.15 (2)	0	0	0.53 (1)	0.18 (1)	0
Flannelmouth sucker	--	0.10 (2)	0.40 (6)	0.88 (1)	0.22 (1)	0	0	0	0
Channel catfish	--	0	0.03 (2)	0.03 (1)	0	0	0	0	0
Unidentified larvae	--	0.35 (2)	0.07 (6)	0.03 (1)	0	0	0.11 (2)	0	0
Total fish	--	0.45	1.85	15.32	0.66	0	0.64	0.18	0

1992									
Category	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Total number of samples	21	105	142	86	52	22	24	23	24
Eggs	75.23 (8)	13.17 (14)	1.72 (14)	5.02 (4)	0.00	0.00	1.69 (6)	0.00	0.76 (6)
Humpback chub	0.49 (1)	0.17 (1)	0.03 (2)	0.00	0.00	0.00	0.00	0.00	0.03 (1)
Speckled dace	0.00	0.00	0.00	0.11 (1)	0.00	0.00	0.00	0.00	0.00

TABLE 4. (continued)

Category	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Bluehead sucker	0.00	0.00	0.05 (3)	0.00	0.00	0.00	0.00	0.00	0.00
Flannelmouth sucker	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03 (1)
Channel catfish	0.00	0.00	0.00	7.81 (8)	0.00	0.00	0.00	0.00	0.00
Unidentified larvae	0.00	0.00	0.01 (1)	0.00	0.00	0.00	0.00	0.00	0.00
Total fish	0.49	0.17	0.09	7.92	0.00	0.00	0.00	0.00	0.05

1993

Category	Apr	May	Jun	Jul
Total number of samples	25	233	208	25
Eggs	0.34 (4)	3.85 (67)	0.26 (20)	0
Humpback chub	0.03 (1)	4.67 (127)	4.05 (34)	0
Speckled dace	0	32.69 (170)	4.38 (75)	0.17 (2)
Bluehead sucker	0	5.36 (94)	2.15 (47)	0.50 (2)
Flannelmouth sucker	0.16 (3)	0.79 (33)	0.23 (10)	0
Channel catfish	0	0.00 (1)	0.04 (10)	0
Fathead minnow	0	1.46 (37)	0.05 (7)	0
Common carp	0	0.46 (19)	0.05 (6)	0
Unidentified larvae	0	2.10 (21)	0.07 (6)	0.17 (1)
Total fish	0.19	47.53	11.10	0.84

TABLE 5. Mean drift densities (numbers/1000 m^3) of fish eggs and larvae (each stage) per diel period, Little Colorado River, 1991-1993, and the Kruskal-Wallis H statistic; * = $p < 0.05$. N = number of drift samples. Mean densities are reported rather than mean ranks for ease of comparison.

Time (hours) Category	0000-0559 (N=168)	0600-1159 (N=235)	1200-1759 (N=232)	1800-2359 (N=222)	H
Eggs	4.32	1.92	3.14	1.70	0.22
Humpback chub	1.41	0.70	1.83	3.26	8.32*
Proto-	0.33	0.19	0.56	0.90	6.66
Meso-	0.82	0.44	0.37	0.47	10.09*
Meta-	0.18	0.07	0.90	1.88	0.88
Speckled dace	12.46	2.27	5.14	9.88	9.55*
Proto-	4.32	0.21	0.33	2.74	14.71*
Meso-	7.77	1.90	4.47	6.90	5.61
Meta-	0.37	0.16	0.34	0.24	1.27
Bluehead sucker	3.00	1.09	1.99	1.96	4.69
Proto-	1.65	0.42	0.65	0.74	10.02*
Meso-	1.13	0.64	1.25	0.98	2.66
Meta-	0.22	0.03	0.08	0.24	8.47*
Flannelmouth sucker	0.29	0.24	0.32	0.36	0.70
Proto-	0.11	0.14	0.03	0.17	0.01
Meso-	0.11	0.11	0.21	0.15	0.51
Meta-	0.07	0.00	0.07	0.04	2.91
Common carp	0.07	0.01	0.04	0.06	3.20
Proto-	0.04	0.00	0.04	0.03	3.70
Meso-	0.03	0.01	0.00	0.03	1.21
Fathead minnow	0.02	0.03	0.03	0.14	1.90
Proto-	0.00	0.00	0.00	0.01	2.86
Meso-	0.02	0.03	0.03	0.13	1.90
Channel Catfish	0.17	0.00	0.00	2.91	8.98*
Meso-	0.00	0.00	0.00	0.00	2.86
Meta-	0.17	0.00	0.00	2.90	7.33

TABLE 6. Mean drift densities (numbers/1000 m^3) of fish eggs and larvae (each stage) at each sampling site, and at near-shore and midchannel placements, Little Colorado River, 1991-1993, and the Kruskal-Wallis H statistic; * = $p < 0.05$. N = number of drift samples. Mean densities are reported rather than mean ranks for ease of comparison.

Category	1.9 km N=560	10.5 km N=447	H	Near-shore N=478	Midchannel N=721	H
Eggs	6.52	1.87	67.45*	1.96	6.03	17.42*
Humpback chub	1.08	2.16	7.42*	3.82	0.27	16.58*
Proto-	0.49	0.37	2.16	1.18	0.12	3.04
Meso-	0.51	0.36	10.57*	1.23	0.12	5.02*
Meta-	0.06	1.43	0.51	1.41	0.01	8.44*
Speckled dace	8.32	2.02	15.82*	15.37	1.94	31.16*
Proto-	1.88	0.14	14.70*	4.02	1.34	4.79*
Meso-	6.31	1.48	19.26	10.65	0.60	21.94*
Meta-	0.13	0.40	0.00	0.56	0.00	15.53*
Bluehead sucker	2.75	0.25	36.86*	3.41	0.20	22.90*
Proto-	1.11	0.12	12.35*	1.35	0.14	2.18
Meso-	1.47	0.07	34.99*	1.80	0.05	25.96*
Meta-	0.16	0.06	3.66	0.26	0.01	12.83*
Flannelmouth sucker	0.45	0.04	27.86*	0.56	0.03	19.09*
Proto-	0.18	0.00	14.61	0.22	0.01	8.42*
Meso-	0.23	0.00	13.69*	0.25	0.02	5.42*
Meta-	0.04	0.04	1.20	0.08	0.00	6.18*
Common carp	0.06	0.00	6.43*	0.12	0.08	0.14
Proto-	0.04	0.00	4.01*	0.09	0.07	1.09
Meso-	0.02	0.00	2.40	0.04	0.01	0.05
Meta-	--	--		0.00	0.00	0.66
Fathead minnow	0.08	0.00	6.43*	0.33	0.27	1.08
Proto-	--	--		0.04	0.10	0.21
Meso-	0.08	0.00	6.43*	0.29	0.17	1.01
Meta-	--	--		0.00	0.00	0.66
Channel catfish	0.10	1.38	3.08	0.04	0.92	2.74
Proto-	0.10	0.00	0.80	0.00	0.00	0.66
Meso-	0.00	0.00	0.03	0.00	0.00	0.82
Meta-	0.10	1.38	3.30	0.04	0.92	1.50

TABLE 7. Logistic regression models for habitat use by YOY native fish in the Little Colorado River. Habitat used by each species is compared to habitat used by the other three species combined. An asterisk indicates $P < 0.05$. V=current velocity (m/s), Z=depth (cm), D = distance from shore (cm), F = feature category (presence of cover coded as "-1", absence of cover coded as "+1"), S = substrate category.

Species	N Used	N Unused	X^2	Logistic regression model					Predictions (% correct) Used	Predictions (% correct) Unused	Predictions (% correct) Total
Base Flow											
BHS	329	328	19.86*	Y= 0.531 (0.145)		- 0.031(Z) (0.007)			69.9	47.6	58.8
FMS	73	73		---------					---	---	---
HBC	172	170	19.56*	Y= 0.979 (0.629)	-14.418(V) (6.266)	+0.031(Z) (0.009)		-0.313(S) (0.135)	55.2	68.2	61.7
SPD	397	398	12.36*	Y= 0.060 (0.104)	+8.006(V) (4.137)		+ 0.234(F) (0.093)		34.5	74.1	54.3
High Flow											
BHS	118	113		---------					---	---	---
FMS	53	54		---------					---	---	---
HBC	77	81		---------					---	---	---
SPD	115	116	4.35*	Y= 0.412 (0.244)		-0.028(Z) (0.014)			42.2	69.6	55.8

TABLE 8. Probabilities of Kruskal-Wallis tests for differences in habitat use among native fish species. Significant differences ($P < 0.05$) are indicated with an asterisk.

	Base Flow			
	Velocity	Depth	Cm_shore	Substrate
Species	0.018*	<0.001*	0.498	0.449
	High Flow			
	Velocity	Depth	Cm_shore	Substrate
Species	0.087	0.149	0.787	0.782

TABLE 9. Nonparametric multiple comparisons (Zar, 1984) for separating significant differences in habitat use among native fish species. No differences were found at high flow (see Table 8). The procedure compares mean ranks of each variable. Q is the test statistic, corrected for ties. * = P < 0.05, ** = P<0.001. BHS=bluehead sucker, FMS=flannelmouth sucker, HBC=humpback chub, SPD=speckled dace.

Base Flow					
Variable	Species	Mean Rank	N	Comparison	Q
Velocity	BHS(B)	480.56	334	B-F	0.290
	FMS(F)	470.38	73	B-H	1.096
	HBC(H)	452.71	174	B-S	2.140
	SPD(S)	523.58	403	F-H	0.466
				F-S	1.539
				H-S	2.875*
Depth	BHS(B)	426.65	336	B-F	2.205
	FMS(F)	507.60	74	B-H	5.954**
	HBC(H)	585.36	175	B-S	4.025**
	SPD(S)	511.58	405	F-H	1.961
				F-S	0.110
				H-S	2.852*

TABLE 10. Percentage use of seven dominant cover categories (BO = boulder, IV = instream vegetation, LE = ledge, OV = overhanging vegetation, TD = turbidity, UB = undercut bank, WD = woody debris). BHS = bluehead sucker, FMS = flannelmouth sucker, HBC = humpback chub, and SPD = speckled dace. Turbidity was not an available cover feature at base flow. N = total number of observations per species.

Species	BO	IV	LE	OV	TD	UB	WD	N
				Base Flow				
BHS	61.7	30.3	0.3	1.8	---	0.9	5.0	1401
FMS	54.8	34.2	0.7	0.0	---	2.1	8.2	281
HBC	49.1	31.1	2.5	4.4	---	2.0	10.9	813
SPD	58.5	28.2	1.1	2.5	---	0.1	9.7	1572
				High Flow				
BHS	60.4	5.2	6.2	0.8	15.6	1.3	10.6	616
FMS	49.3	12.7	3.4	3.4	20.1	0.0	11.2	268
HBC	45.1	18.3	4.8	1.5	13.5	2.8	14.0	399
SPD	73.8	8.7	2.3	0.0	10.6	0.5	4.1	435

TABLE 11. Probabilities of Kruskal-Wallis tests for differences in habitat use within species, among larval stages. Cm_shore = distance from shore; substrate includes five ordinal categories (see text). Significant differences ($P < 0.05$) are indicated with an asterisk.

Species	Flow	Depth	Cm_shore	Substrate
		Base Flow		
BHS	<0.001*	<0.001*	<0.001*	0.012*
FMS	0.728	0.024*	0.194	0.146
HBC	0.319	0.184	0.489	0.627
SPD	0.276	<0.001*	0.300	0.098
		High flow		
BHS	0.118	0.126	0.039*	0.211
FMS	0.030*	0.939	0.649	0.211
HBC	0.287	0.379	0.129	0.627
SPD	0.091	<0.001*	0.786	0.020*

TABLE 12. Nonparametric multiple comparisons (Zar 1984) for separating significant differences in habitat use within species, among larval stages: 1 = protolarvae, 2 = mesolarvae, and 3 = metalarvae. N = number of fish observed. The procedure compares mean ranks of each variable; Q is the test statistic, corrected for ties. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.005$. Q-values for comparisons involving fewer than 10 fish are not shown.

Variable	Species	Larval stage	Mean Rank	N	Comparison	Q
			Base Flow			
Flow	BHS	1	137.38	120	1-2	2.90*
		2	168.89	150	2-3	2.25
		3	200.57	54	1-3	4.34***
Depth	BHS	1	134.01	120	1-2	2.82*
		2	166.48	152	2-3	3.63***
		3	220.66	54	1-3	5.61***
	FMS	1	27.71	19	1-2	1.72
		2	37.80	42	2-3	1.60
		3	48.92	12	1-3	2.71*
	SPD	1	42.63	4	1-2	---
		2	79.60	24	2-3	3.02**
		3	123.91	207	1-3	---
Cm_shore	BHS	1	132.87	120	1-2	3.16***
		2	169.20	152	2-3	3.11**
		3	215.54	54	1-3	5.36***
Substrate	BHS	1	156.39	119	1-2	1.78
		2	174.04	150	2-3	2.84*
		3	137.50	58	1-3	1.42

TABLE 12. (continued)

Variable	Species	Larval stage	Mean Rank	N	Comparison	Q
			High Flow			
Flow	FMS	1	32.56	24	1-2	2.23
		2	23.00	28	2-3	---
		3	5.50	1	1-3	---
Depth	SPD	1	42.17	12	1-2	0.72
		2	50.53	43	2-3	3.20***
		3	72.75	68	1-3	2.74*
Cm_shore	BHS	1	55.05	60	1-2	2.54*
		2	71.75	63	2-3	---
		3	59.33	3	1-3	---
Substrate	SPD	1	60.58	12	1-2	0.91
		2	70.24	42	2-3	2.80*
		3	52.25	64	1-3	0.82

TABLE 13. Behavioral time budgets (% of total seconds) by length category (mm) for humpback chub, speckled dace, bluehead sucker, and flannelmouth sucker, Little Colorado River. H is the Kruskal-Wallis statistic; * = $P < 0.05$.

	Humpback Chub				Speckled Dace			
	≤30	31-50	51-100	H	≤30	31-50	51-100	H
Feeding								
Total	26.8	8.9	13.3	12.46*	12.7	3.8	16.8	8.64*
Bottom	22.6	3.5	6.5	21.04*	10.7	0.1	2.6	13.33*
Plant	1.1	0.3	0.9	0.04	0.9	0.1	2.5	6.09*
Column	0.4	0.4	1.9	1.31	0.2	0.1	3.7	4.76
Surface	2.7	4.7	4.0	0.32	0.9	3.6	8.1	15.68*
Nonfeeding								
Total	73.2	91.9	86.7	12.46*	87.3	96.2	83.2	8.64*
Swim	69.3	87.0	76.8	7.19*	80.6	86.8	53.9	11.72*
School	1.4	1.4	1.5	1.61	5.2	0.0	0.2	1.68
Chasing	0.4	0.7	1.3	2.10	0.0	1.9	5.1	5.68
Chased by	0.5	0.4	0.3	13.18*	0.2	0.3	0.8	0.36
Other	1.5	1.6	6.8	4.13	1.3	7.3	23.2	12.58*
Total Seconds	6326	19854	12383		13047	1566	2257	
N	23	74	45		48	6	11	

TABLE 13. (continued)

	Bluehead Sucker				Flannelmouth Sucker		
	≤30	31-50	51-100	H	≤30	31-50	H
Feeding							
Total	26.0	46.5	38.3	7.65*	47.8	34.8	0.12
Bottom	19.6	36.8	27.0	3.69	27.3	0.0	5.07*
Plant	4.0	9.2	9.2	4.25	0.7	0.1	0.10
Column	1.9	0.1	1.3	3.46	0.1	0.0	0.29
Surface	0.6	0.4	0.8	1.35	19.8	38.3	3.76
Nonfeeding							
Total	74.0	53.5	61.7	7.65*	52.2	65.2	0.12*
Swim	67.9	30.4	30.1	19.62*	44.7	39.4	0.31
School	3.0	2.8	1.2	3.27	6.1	21.6	4.66*
Chasing	0.2	0.0	0.0	4.50	0.5	0.0	0.62
Chased by	0.1	0.0	0.0	6.93*	0.0	0.2	0.18
Other	2.8	20.4	30.4	16.01*	0.8	0.5	0.21
Total							
Seconds	19817	5594	2185		10218	1333	
N	68	21	12		39	5	

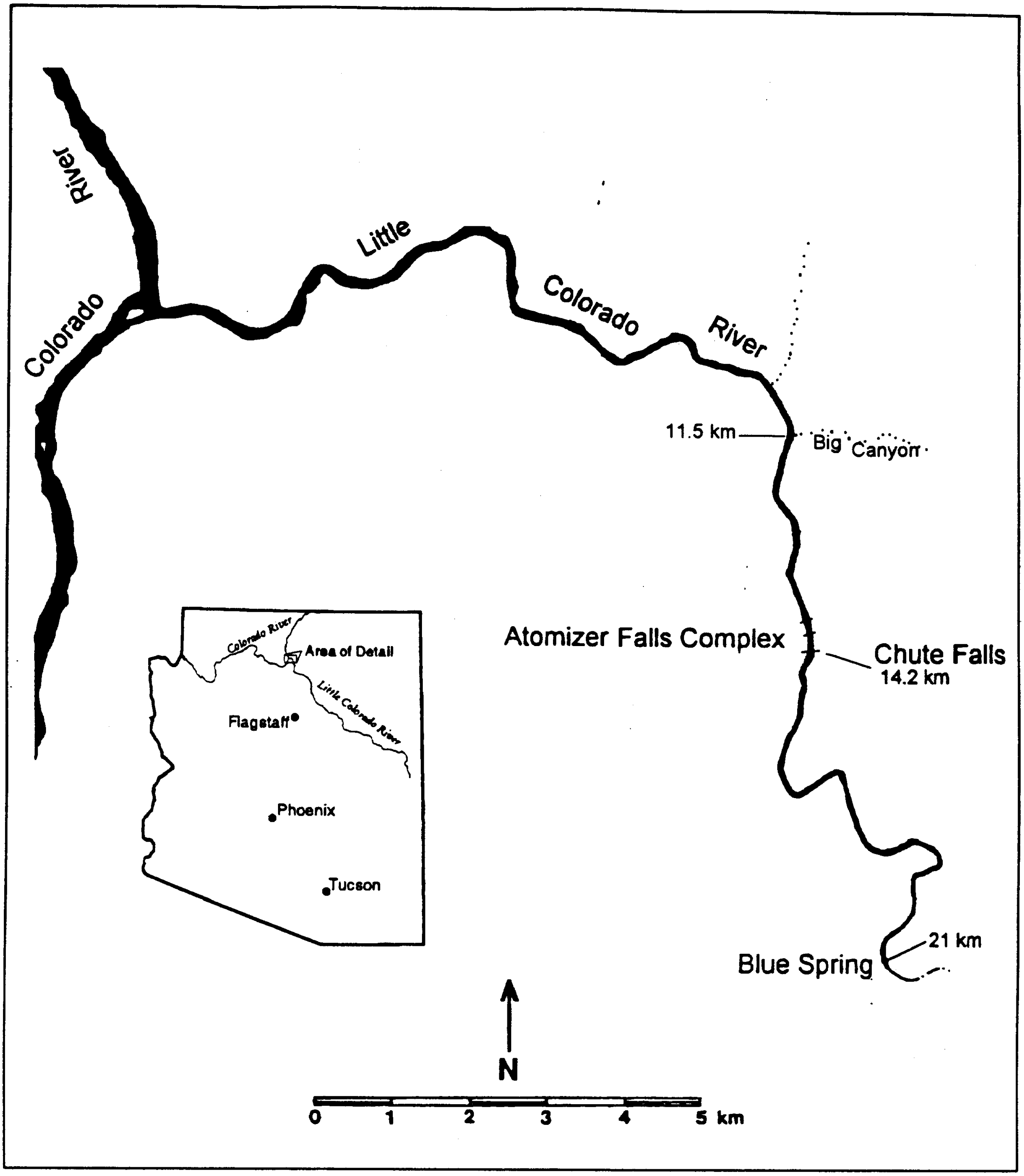


FIGURE 1. Map of the study area; the terminal, perennial 21 km of the Little Colorado River, Arizona.

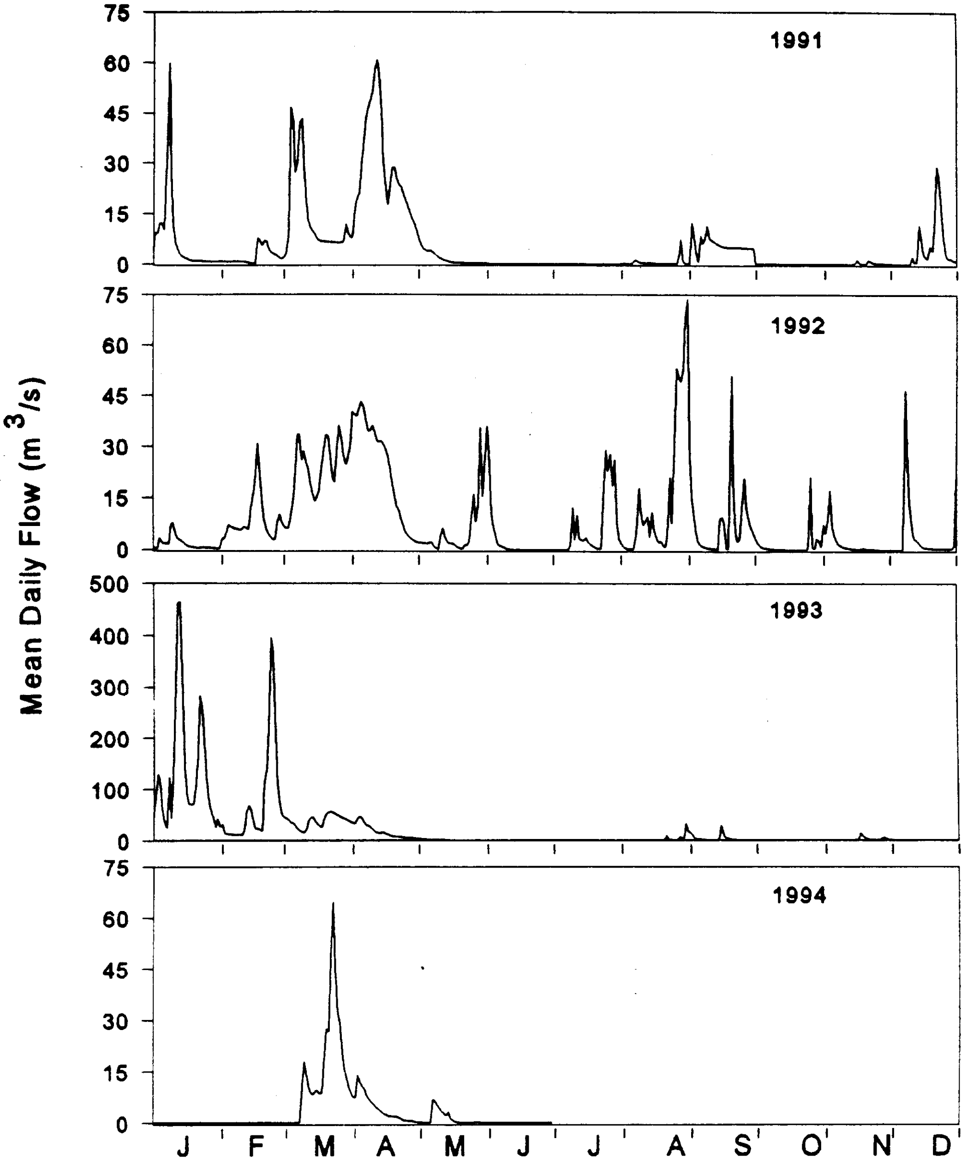


FIGURE 2. Mean daily flow (m^3/s) of the Little Colorado River recorded at the USGS gauging station near Cameron, Arizona.

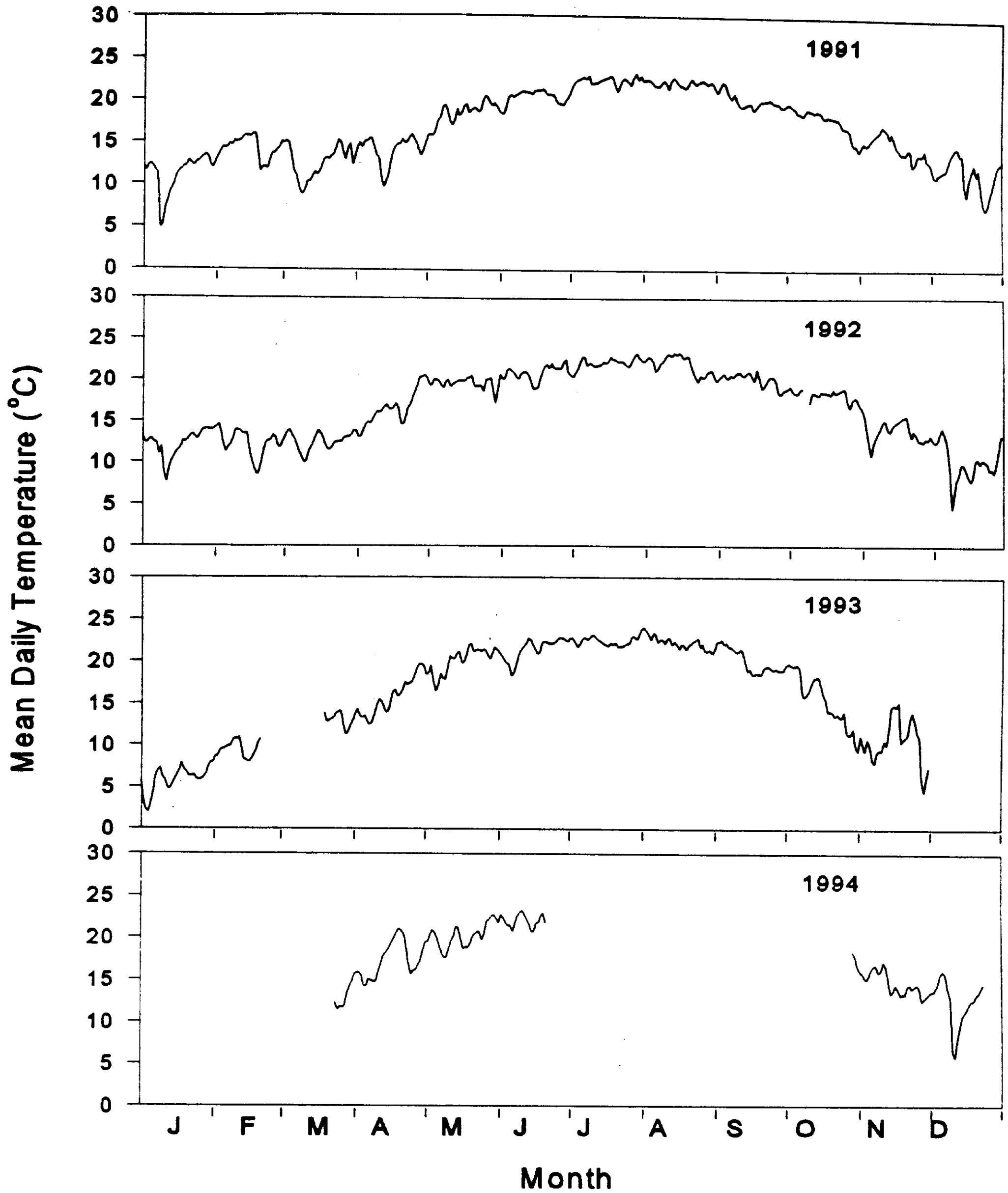


FIGURE 3. Mean daily water temperatures (°C) recorded approximately one mile above the mouth, Little Colorado River, Arizona, 1991-1994.

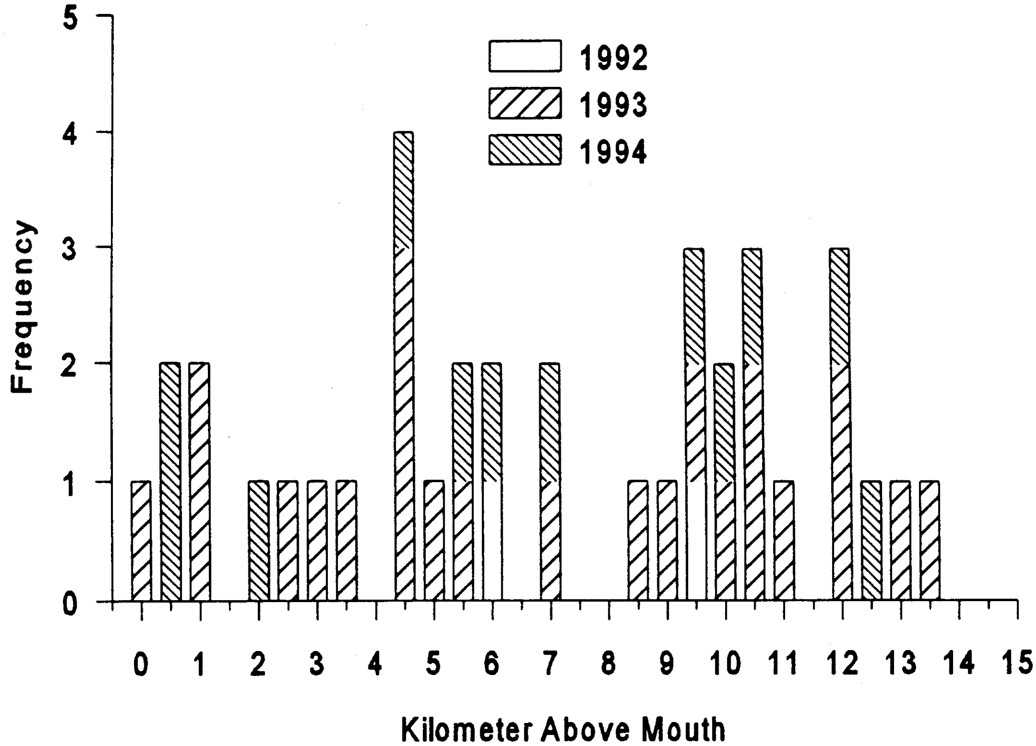


FIGURE 4. Frequency of encounters of humpback chub protolarvae per kilometer in longitudinal surveys.

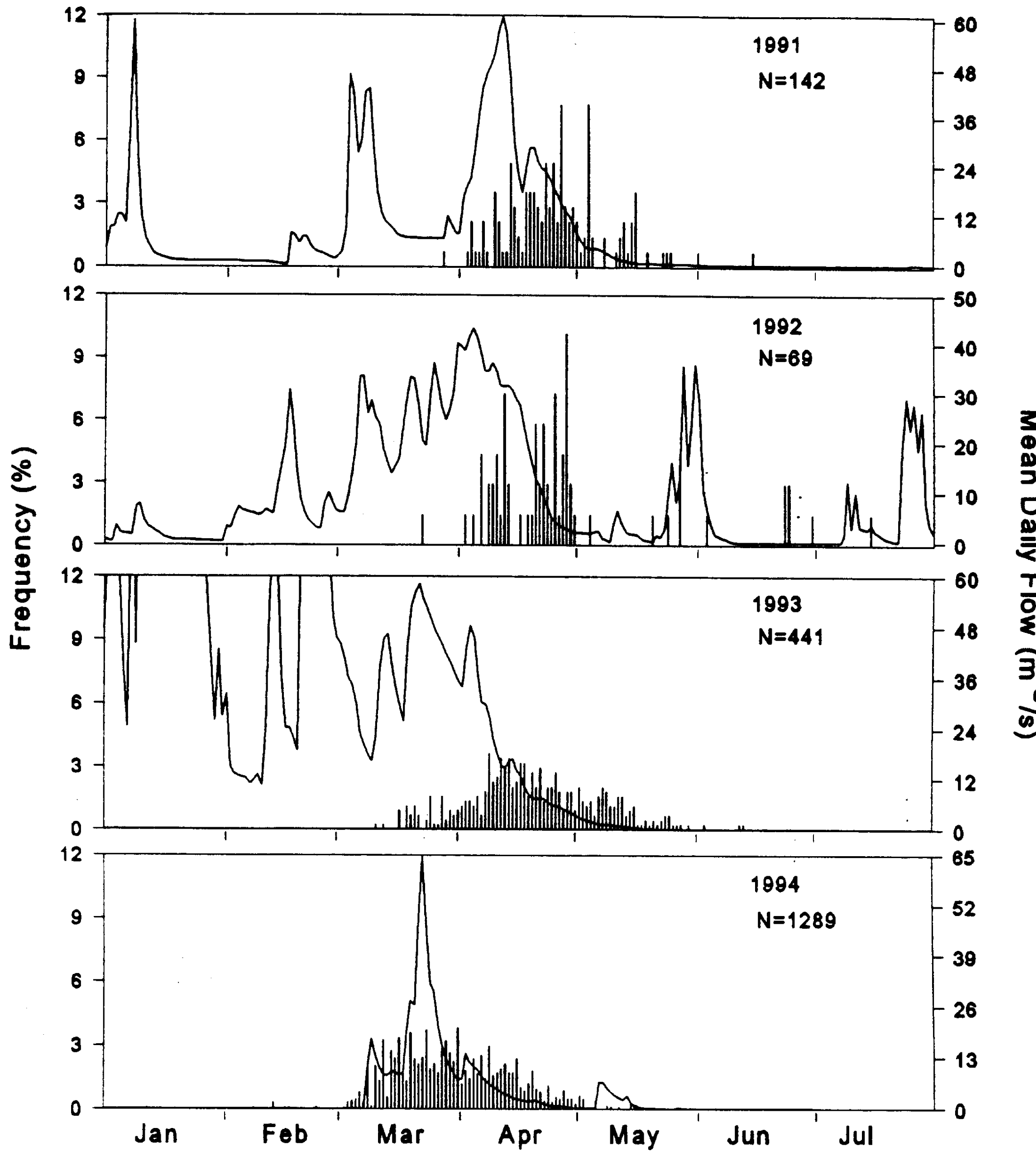


FIGURE 5. Estimated frequency of spawning date (bars) for humpback chub, and mean daily flow (m^3/s; recorded at Cameron AZ), Little Colorado River, 1991-1994. Estimated spawning dates are back-calculated from larval lengths.

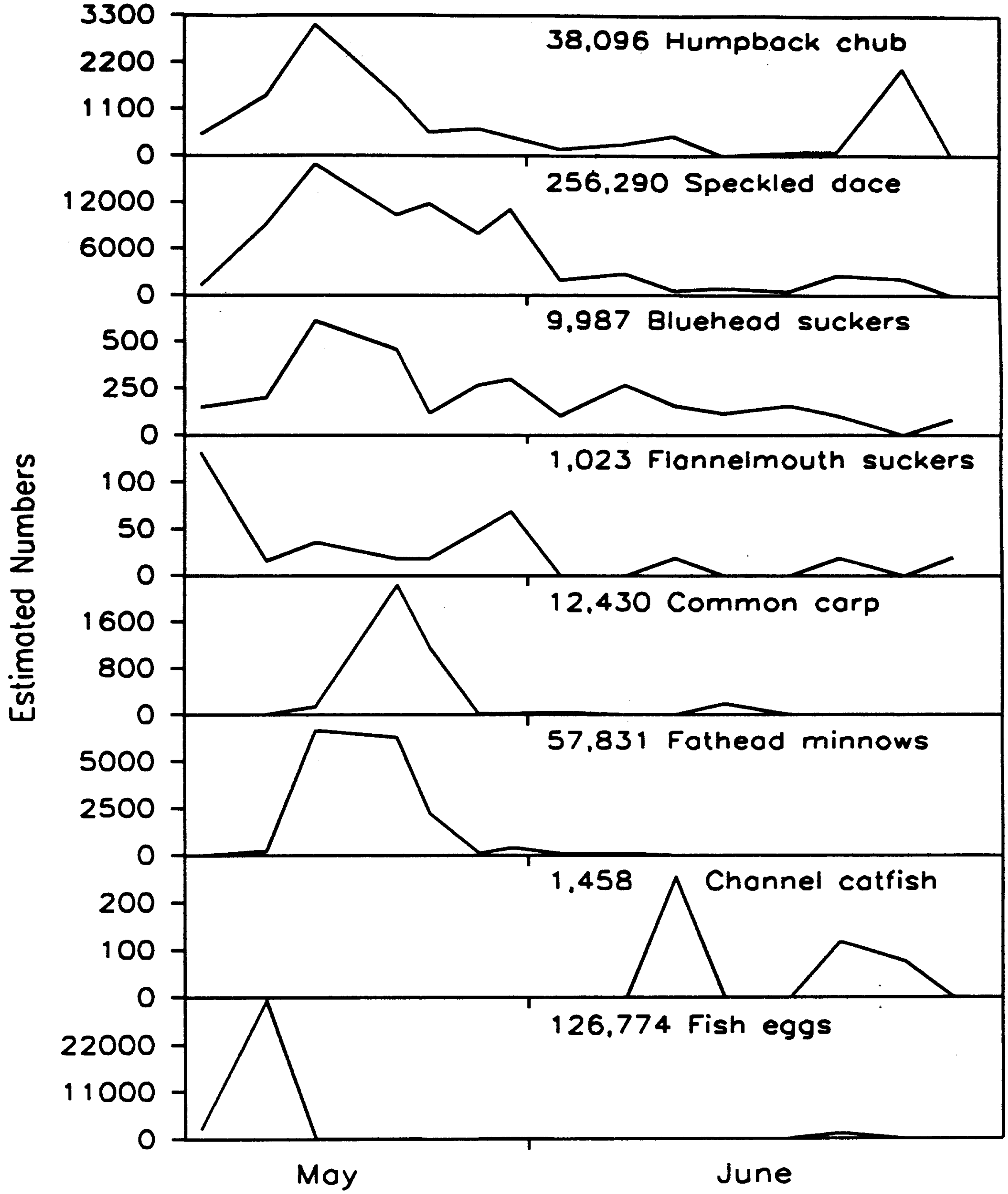


FIGURE 6. Estimated numbers of fish larvae and eggs transported out of the Little Colorado River, May 11-June 26, 1993.

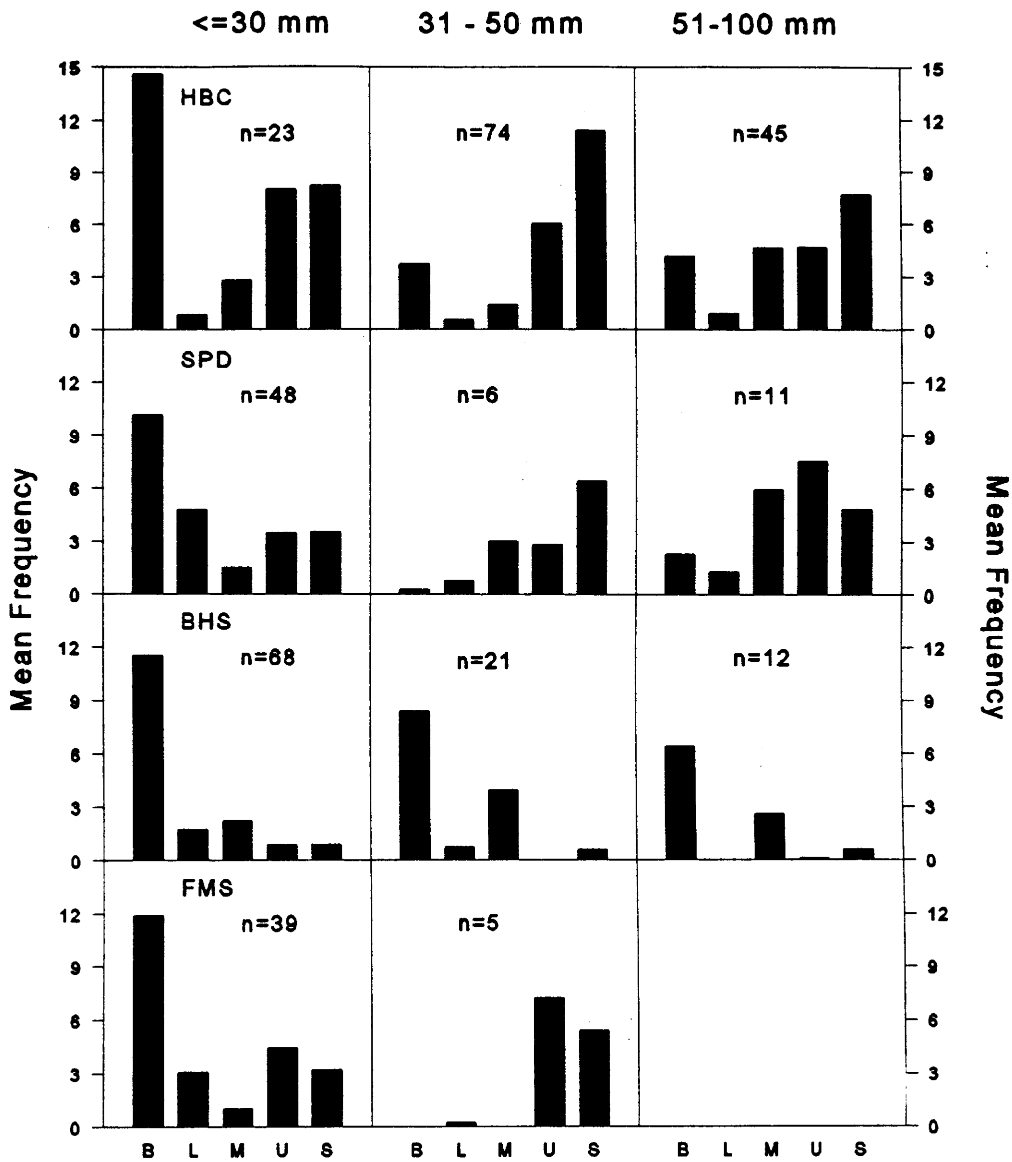
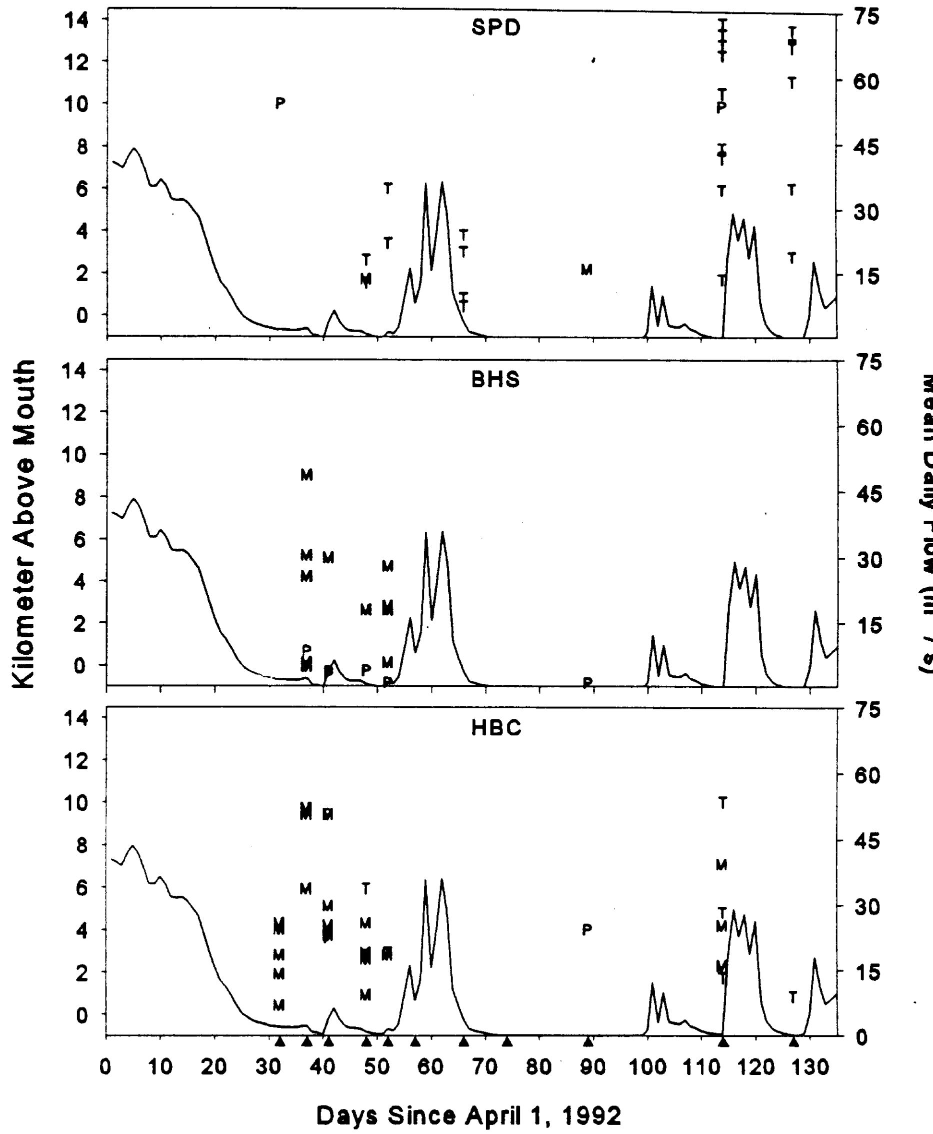


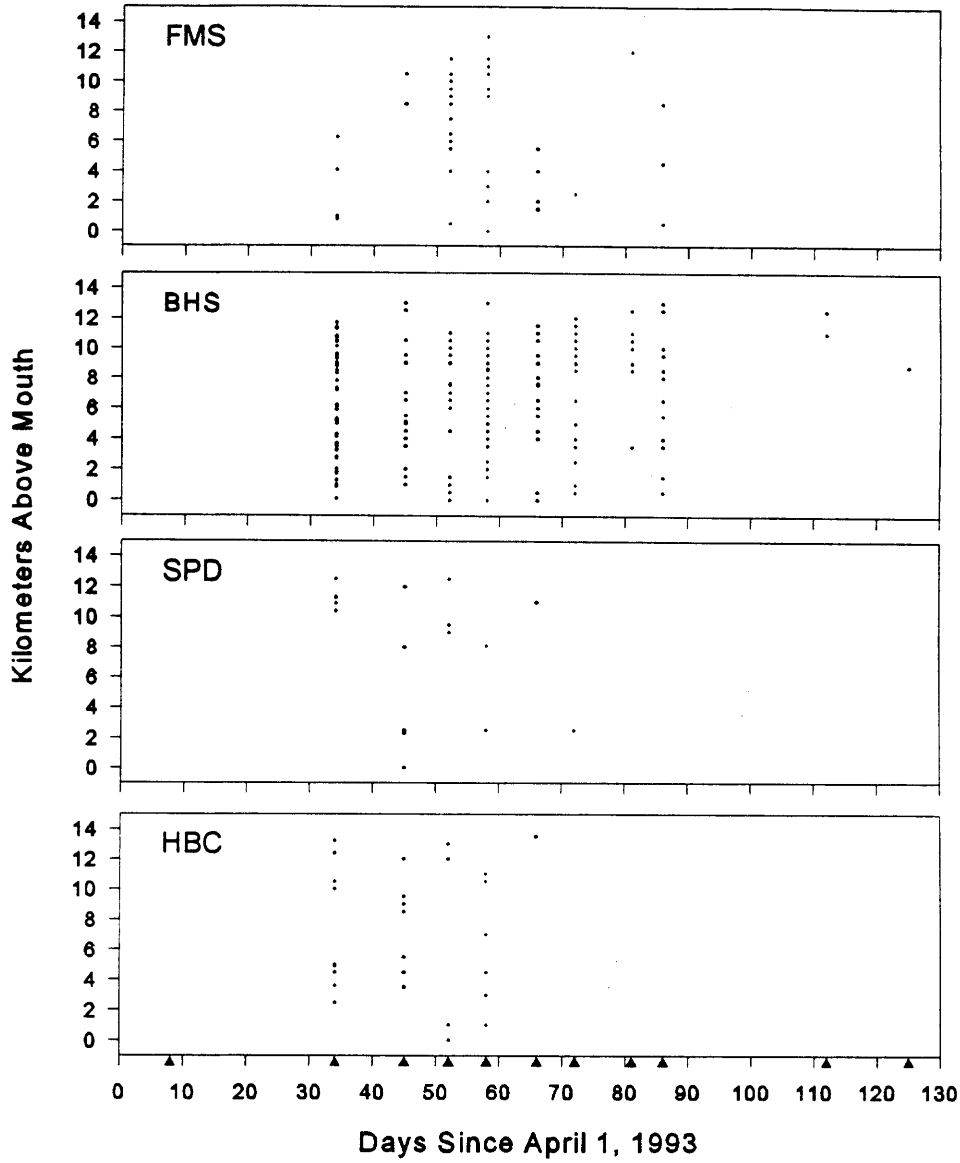
FIGURE 7. Frequency of use of five water column categories for three length categories of YOY native fishes during behavioral observations, Little Colorado River, 1992-1994. HBC=humpback chub, SPD=speckled dace, BHS=bluehead sucker, FMS=flannelmouth sucker, B=bottom, L=lower pelagic, M=mid-pelagic, U=upper pelagic, S=surface. n=number of fish observed.

APPENDIX I

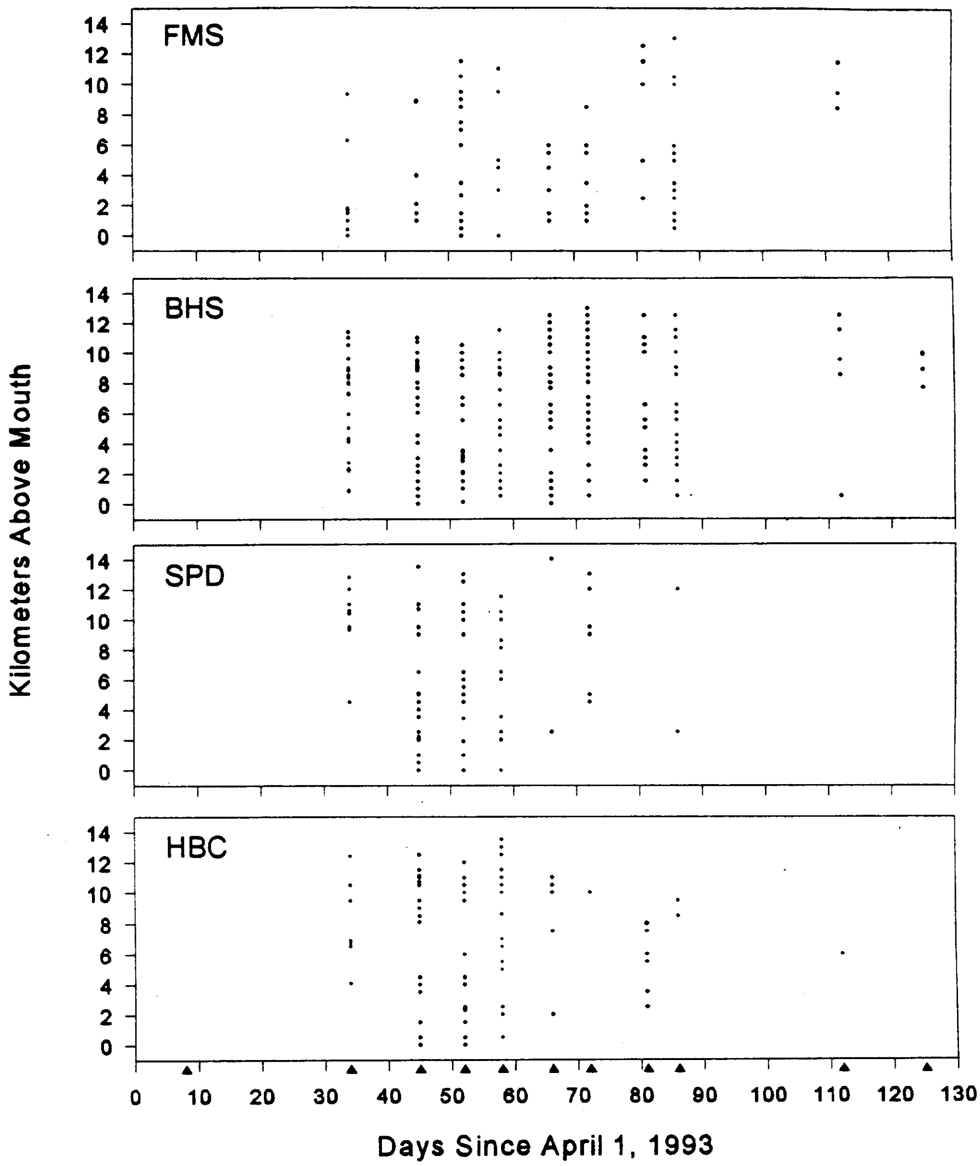
SPATIAL AND TEMPORAL DISTRIBUTIONS OF LARVAE



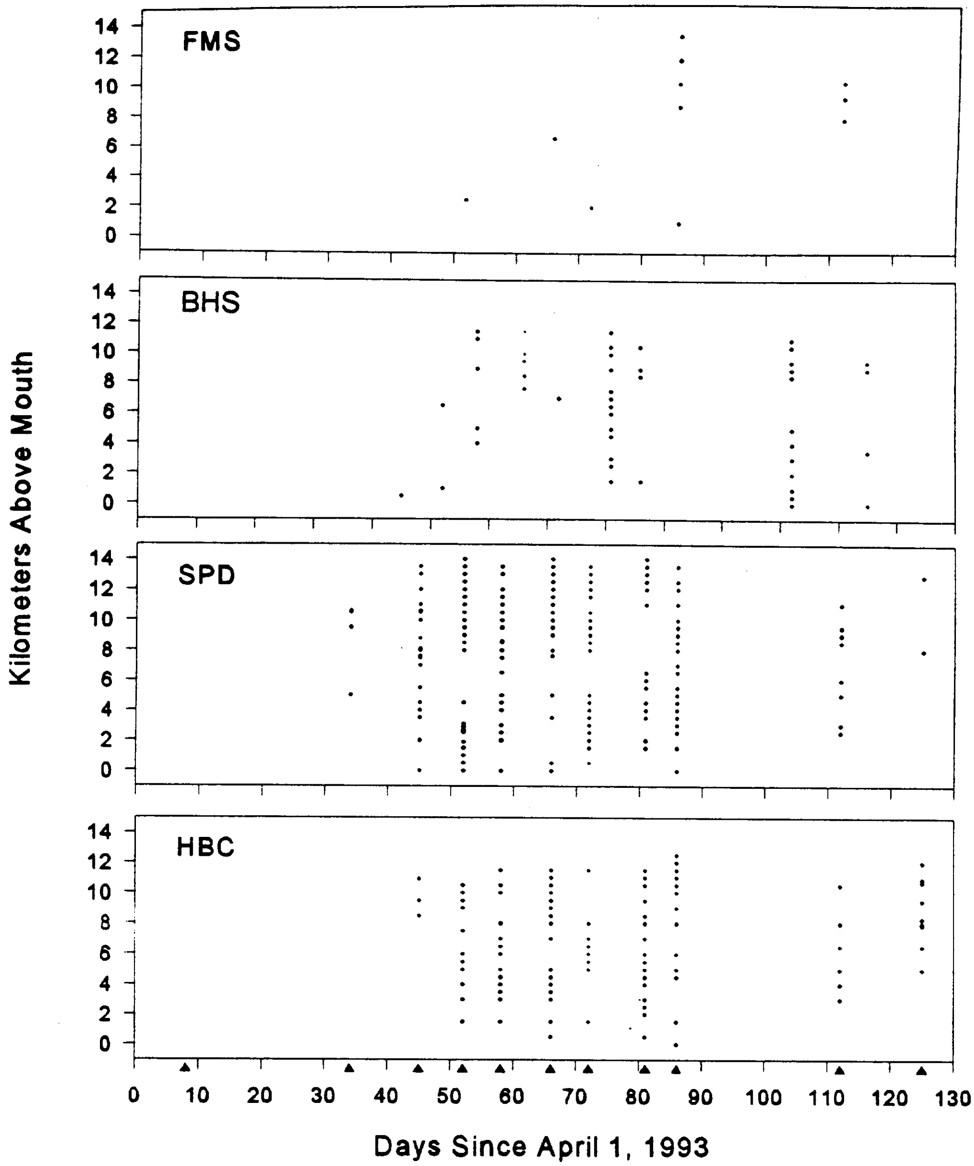
APPENDIX I a. Longitudinal and temporal distributions of larvae, and mean daily flow (m^3/s; Cameron AZ), Little Colorado River, 1992. Presence of larvae in each kilometer (km) for each longitudinal survey, is shown the final day of each survey (indicated by "▲"). Symbols indicate the following larval stages: P = protolarvae, M = mesolarvae, T = metalarvae. BHS = bluehead sucker, SPD = speckled dace, HBC = humpback chub.



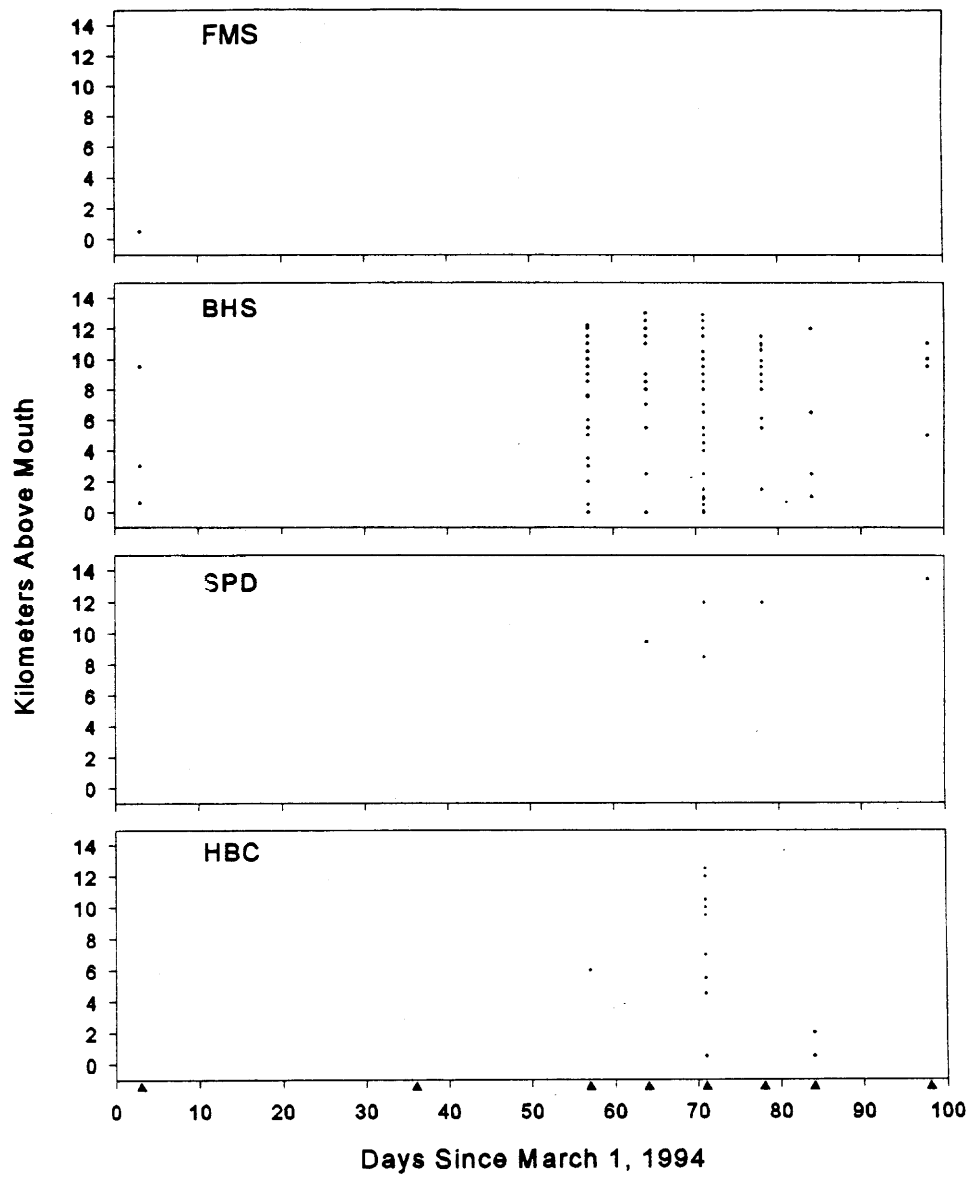
APPENDIX I b. Longitudinal and temporal distributions of protolarvae, Little Colorado River, 1993. Presence of larvae in each km for each longitudinal survey, is shown the final day of each survey (indicated by "▲"). FMS = flannelmouth sucker, BHS = bluehead sucker, SPD = speckled dace, HBC = humpback chub.



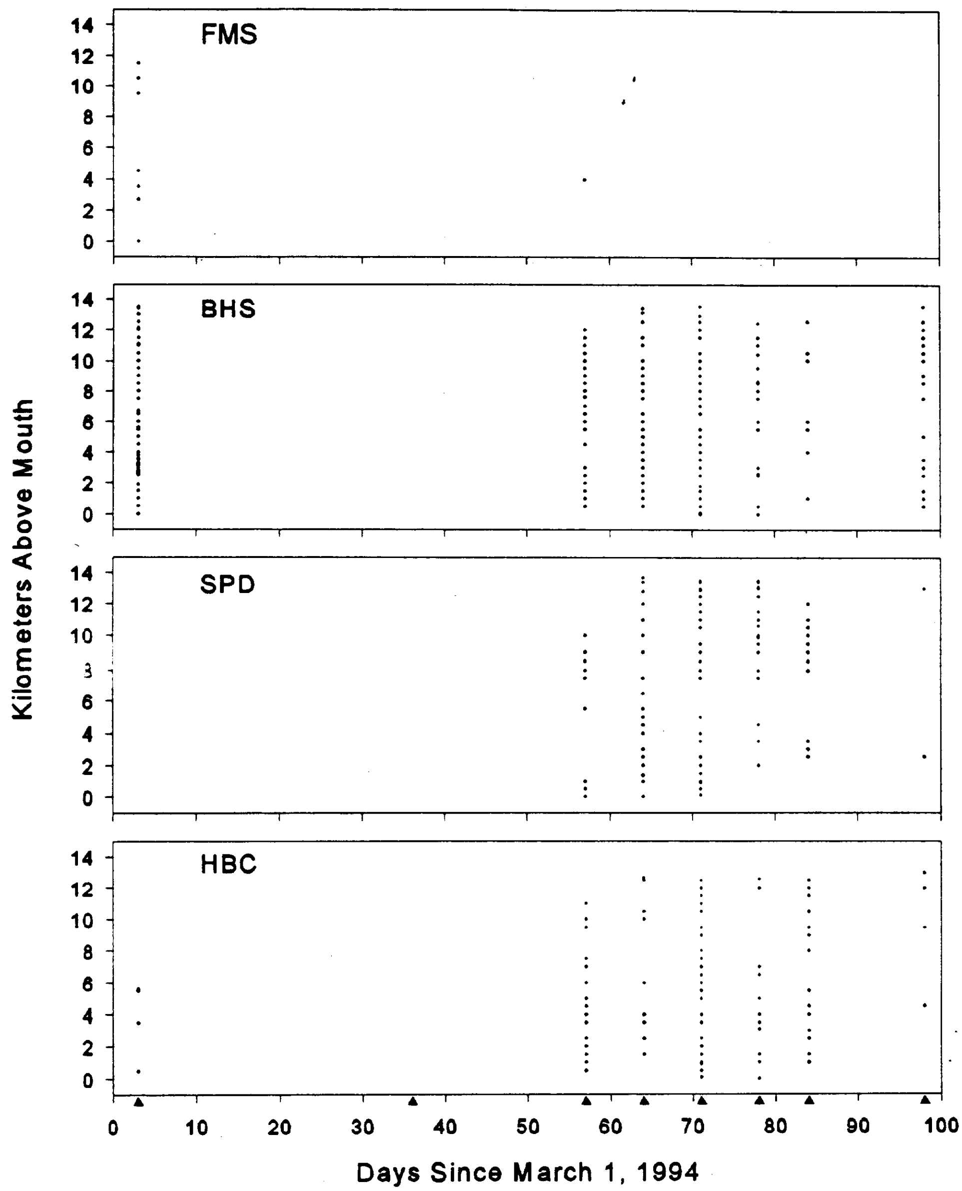
APPENDIX I c. Longitudinal and temporal distributions of mesolarvae, Little Colorado River, 1993. Presence of larvae in each km for each longitudinal survey, is shown the final day of each survey (indicated by "▲"). See Appendix I b for species codes.



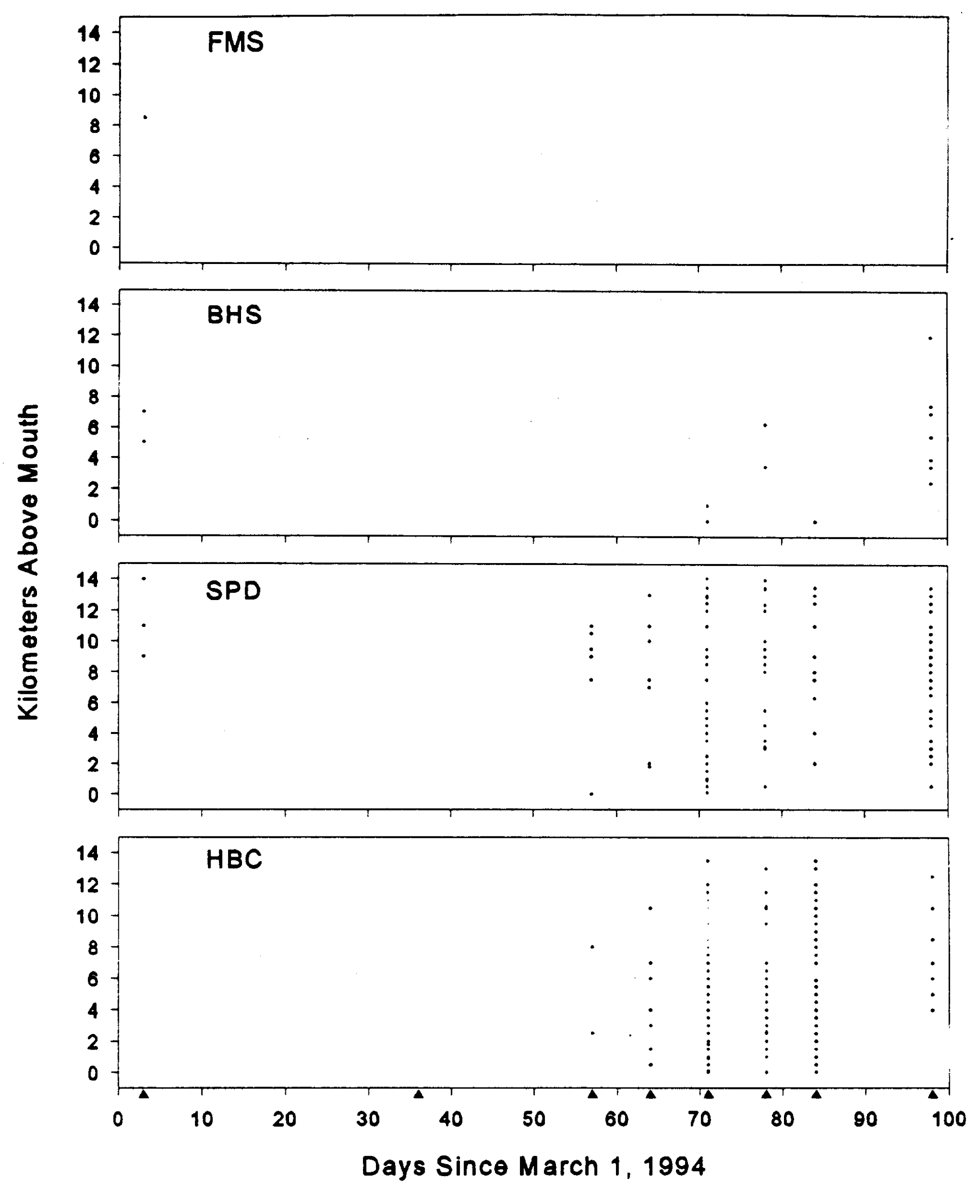
APPENDIX I d. Longitudinal and temporal distributions of metalarvae, Little Colorado River, 1993. Presence of larvae in each km for each longitudinal survey, is shown the final day of each survey (indicated by "▲"). See Appendix I b for species codes.



APPENDIX I e. Longitudinal and temporal distributions of protolarvae, Little Colorado River, 1994. Presence of larvae in each km for each longitudinal survey, is shown the final day of each survey (indicated by "▲"). See Appendix I b for species codes.



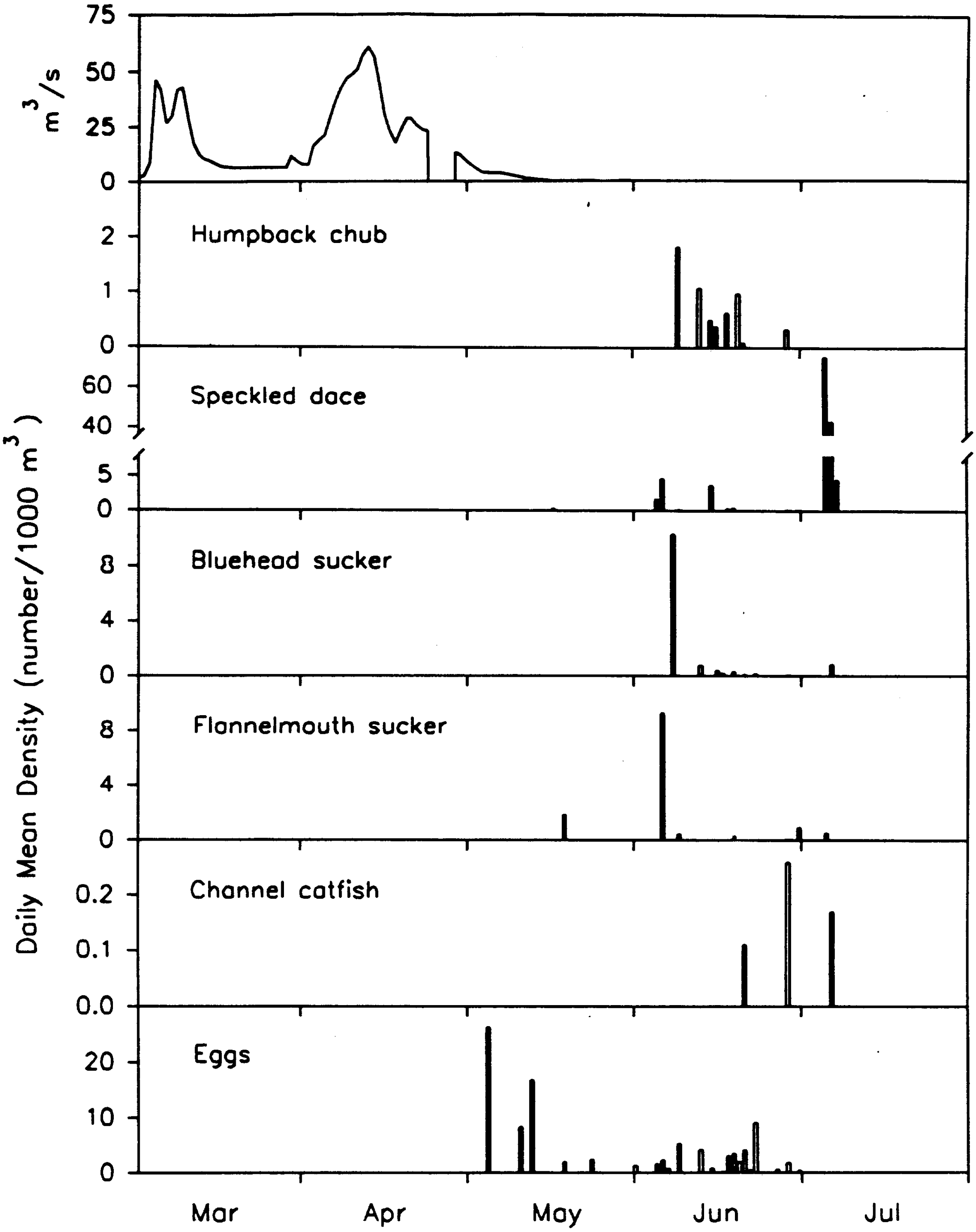
APPENDIX I f. Longitudinal and temporal distributions of mesolarvae, Little Colorado River, 1994. Presence of larvae in each km for each longitudinal survey, is shown the final day of each survey (indicated by "▲"). See Appendix I b for species codes.



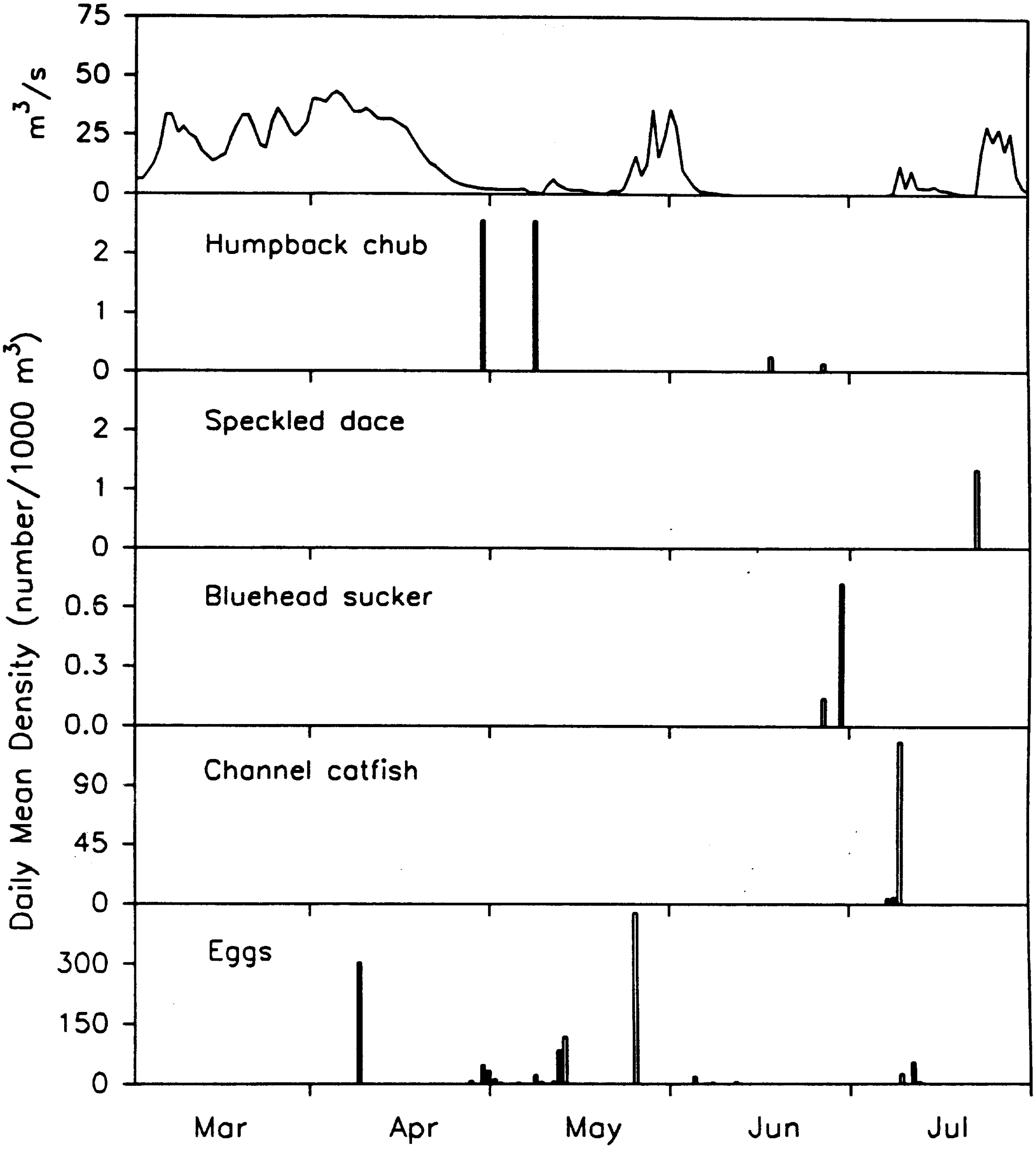
APPENDIX I g. Longitudinal and temporal distributions of metalarvae, Little Colorado River, 1994. Presence of larvae in each km for each longitudinal survey, is shown the final day of each survey (indicated by "▲"). See Appendix I b for species codes.

APPENDIX II

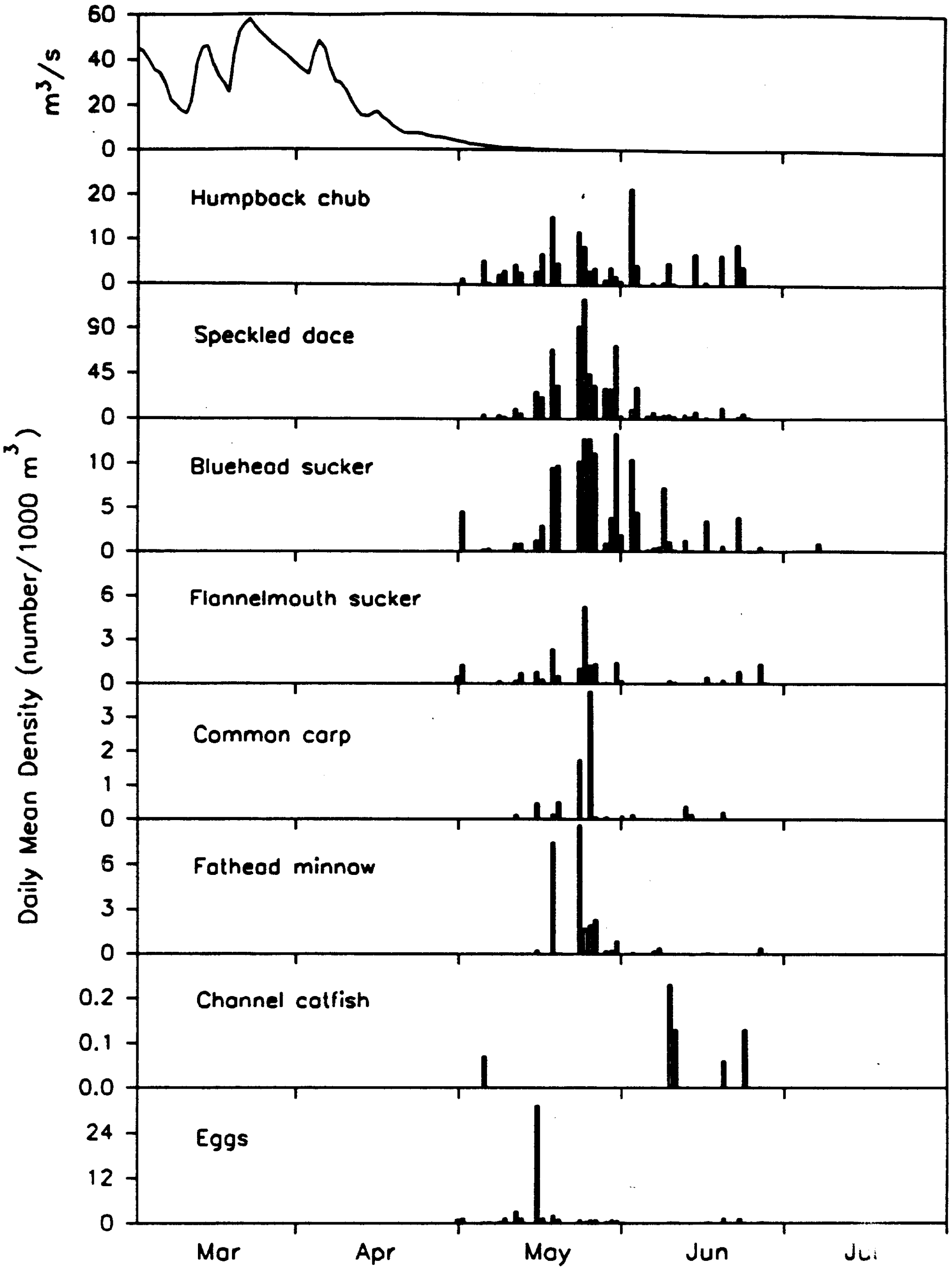
TIMING OF LARVAL AND EGG DRIFT



APPENDIX II a. Mean daily flow (m^3/s; Cameron, AZ) and mean drift densities of fish larvae and eggs, Little Colorado River, 1991. Sampling began May 4.



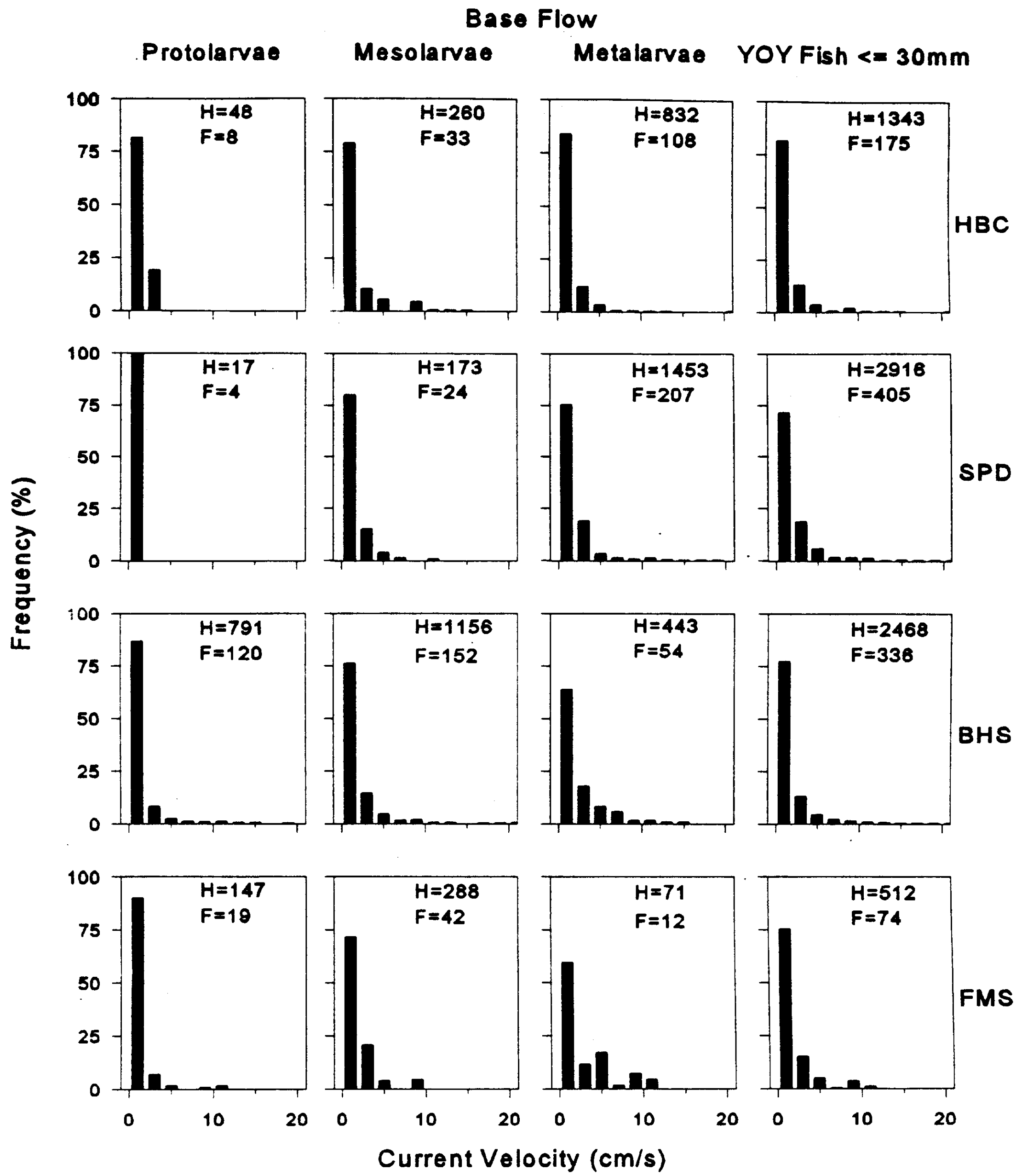
APPENDIX II b. Mean daily flow (m^3/s; Cameron, AZ) and mean drift densities of fish larvae and eggs during the spawning period, Little Colorado River, 1992.



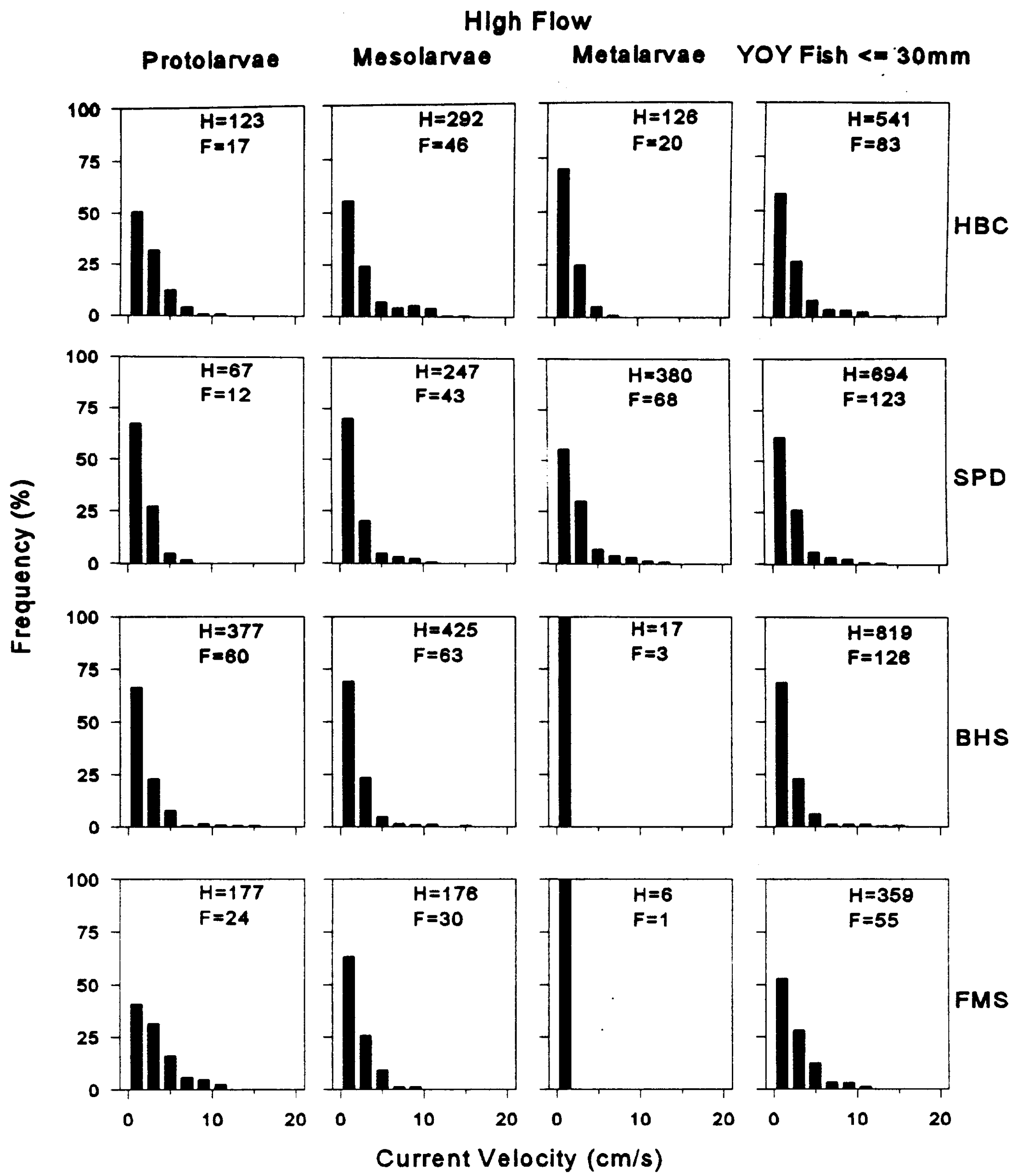
APPENDIX II c. Mean daily flow (m^3/s; Cameron, AZ) and mean drift densities of fish larvae and eggs during the spawning period, Little Colorado River, 1993.

APPENDIX III

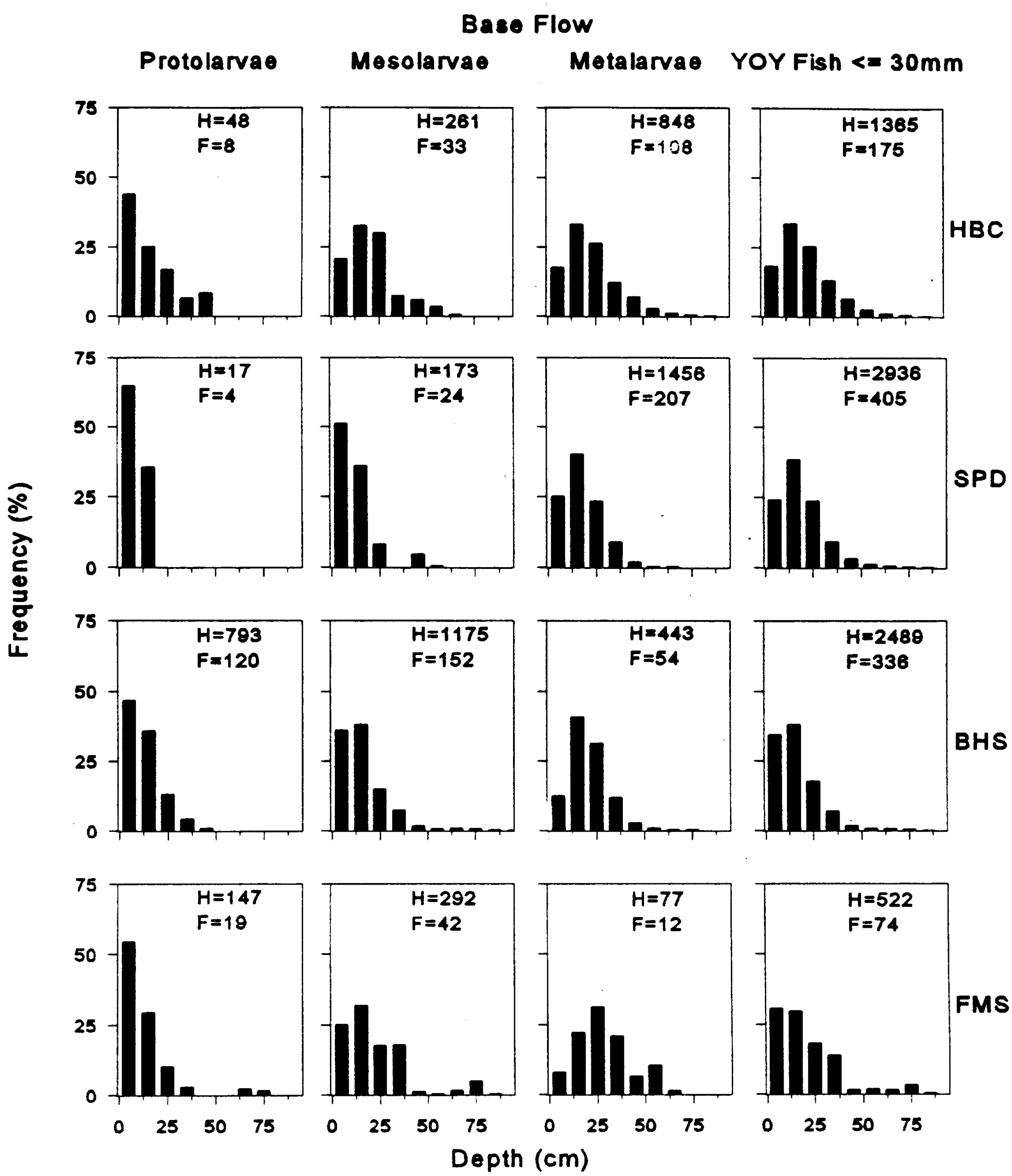
HABITAT USE BY LARVAE



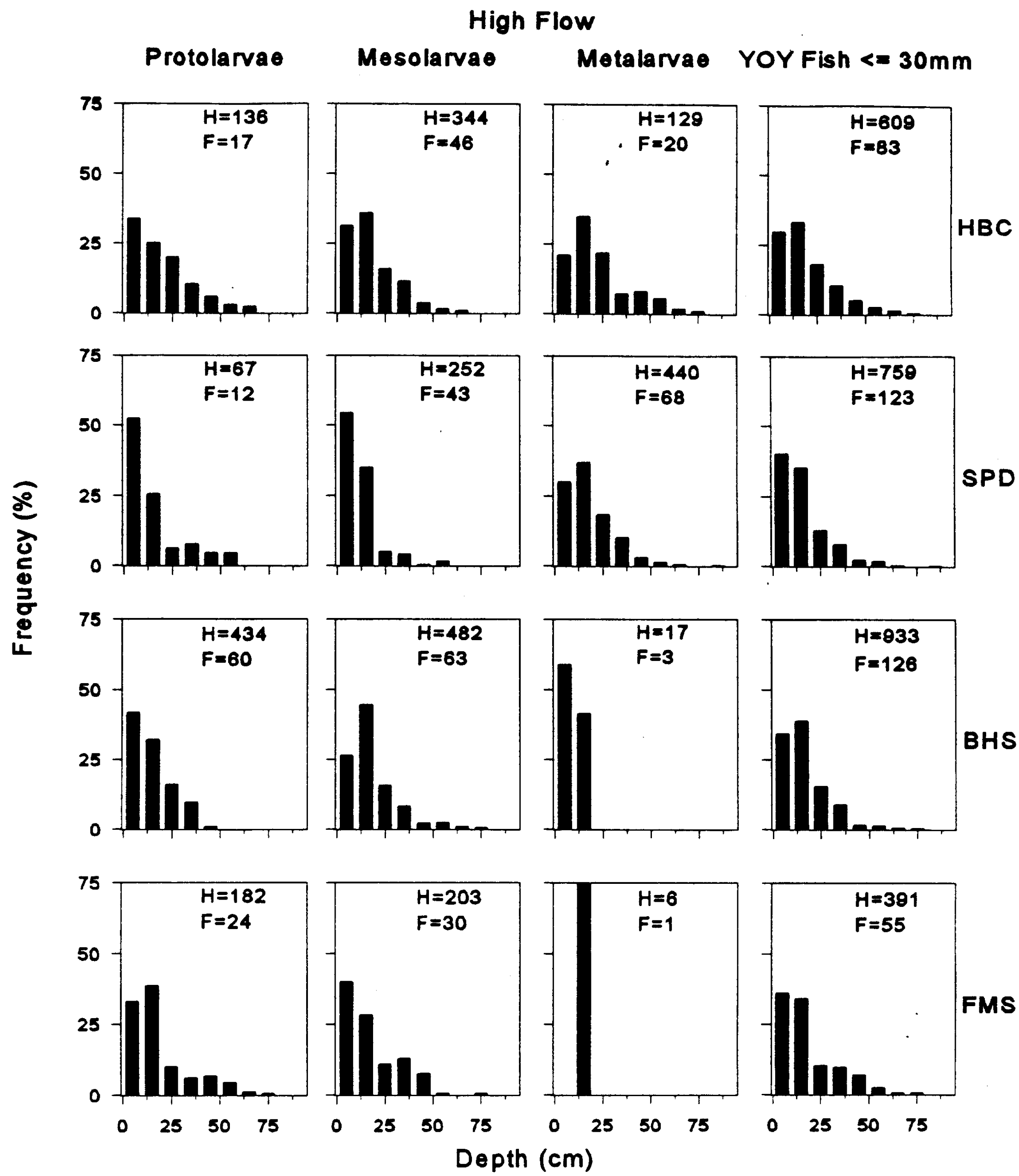
APPENDIX III a. Frequency of current velocities used by larval and YOY fish in LCR near-shore habitats at base flow, 1993. H = number of habitat points sampled; F = number of fish collected.



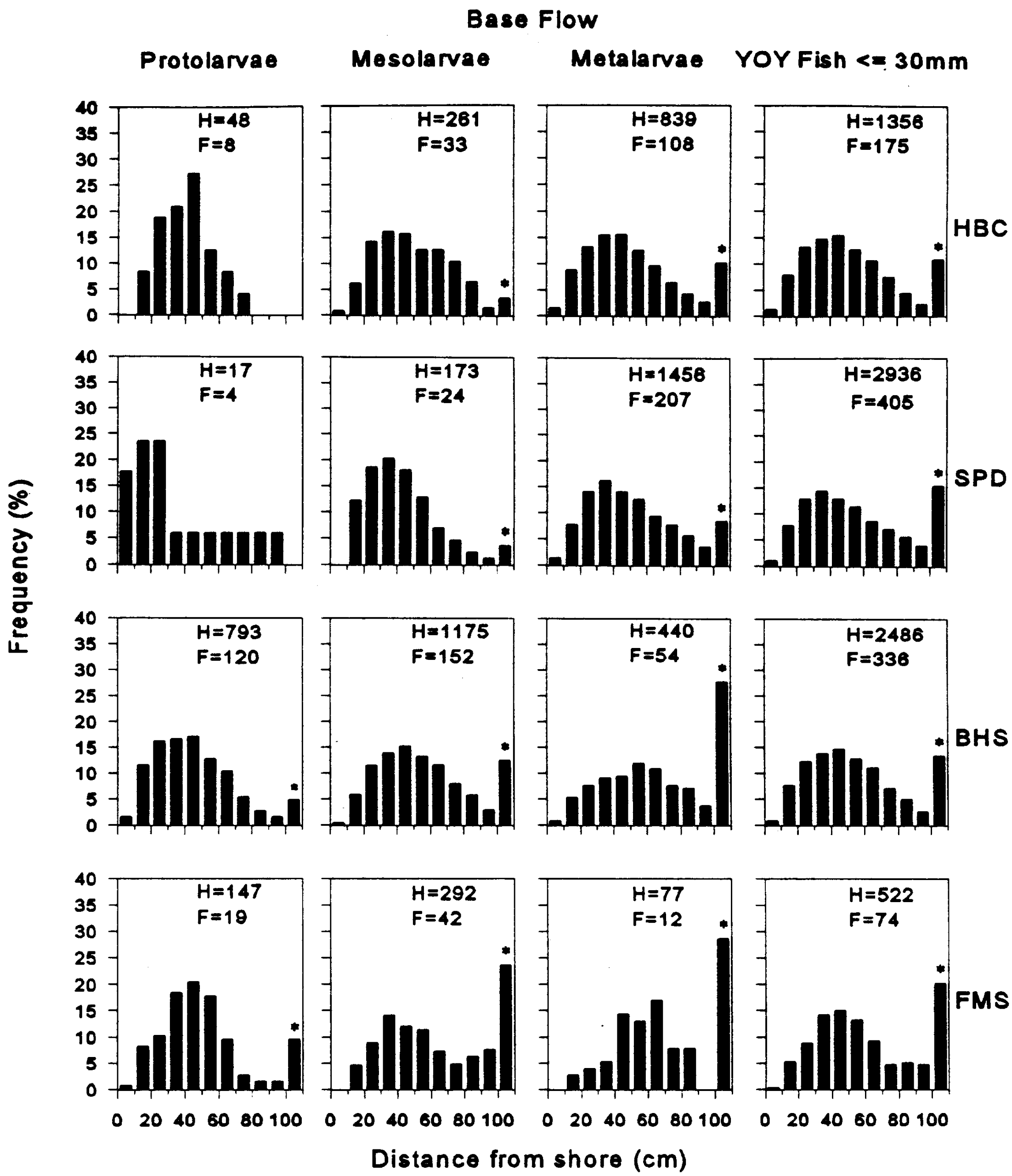
APPENDIX III b. Frequency of current velocities used by larval and YOY fish in LCR near-shore habitats at high flow, 1993. H = number of habitat points sampled; F = number of fish collected.



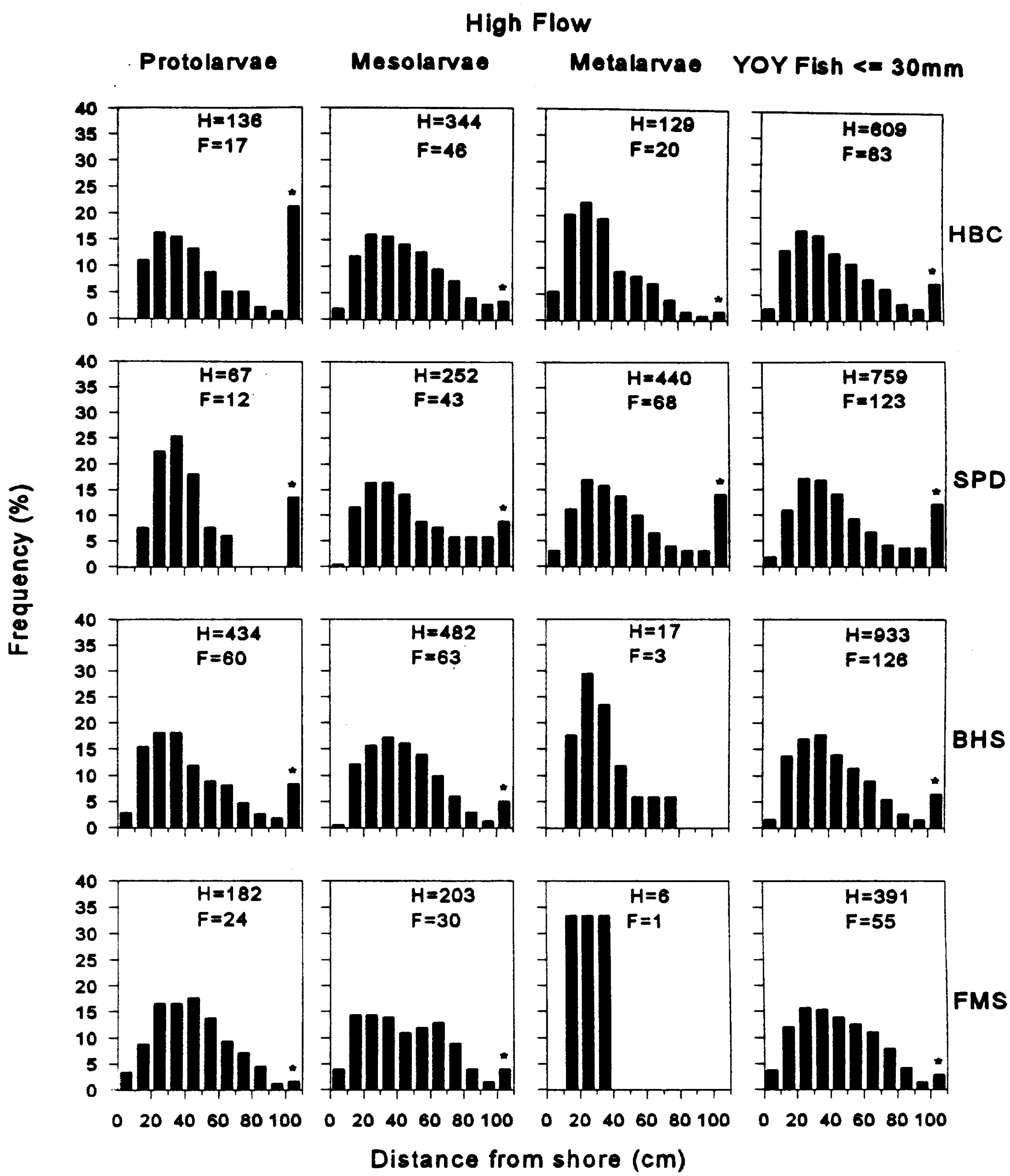
APPENDIX III c. Frequency of depths used by larval and YOY fish in LCR near-shore habitats at base flow, 1993. H = number of habitat points sampled; F = number of fish collected.



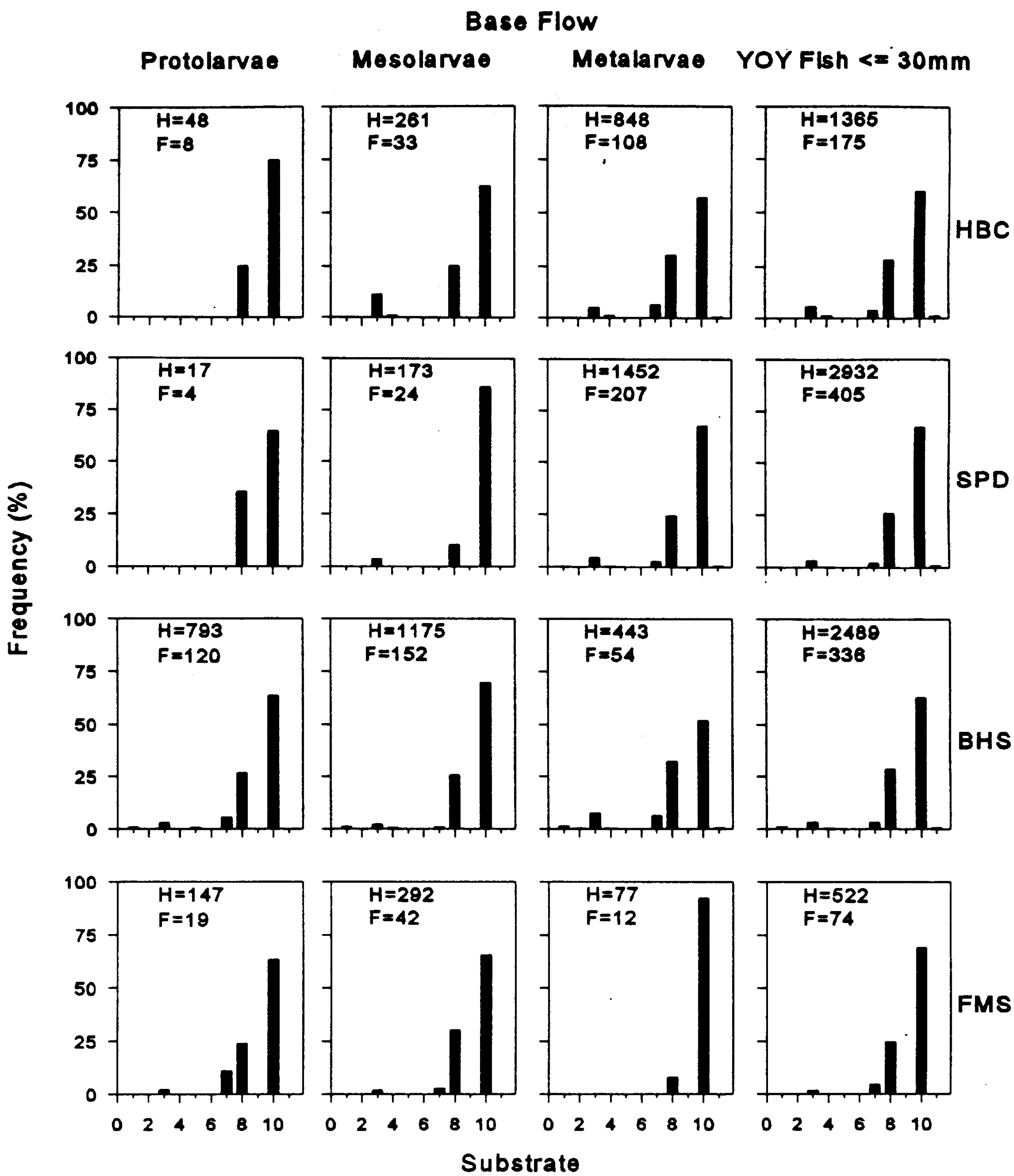
APPENDIX III d. Frequency of depths used by larval and YOY fish in LCR near-shore habitats at high flow, 1993. H = number of habitat points sampled; F = number of fish collected.



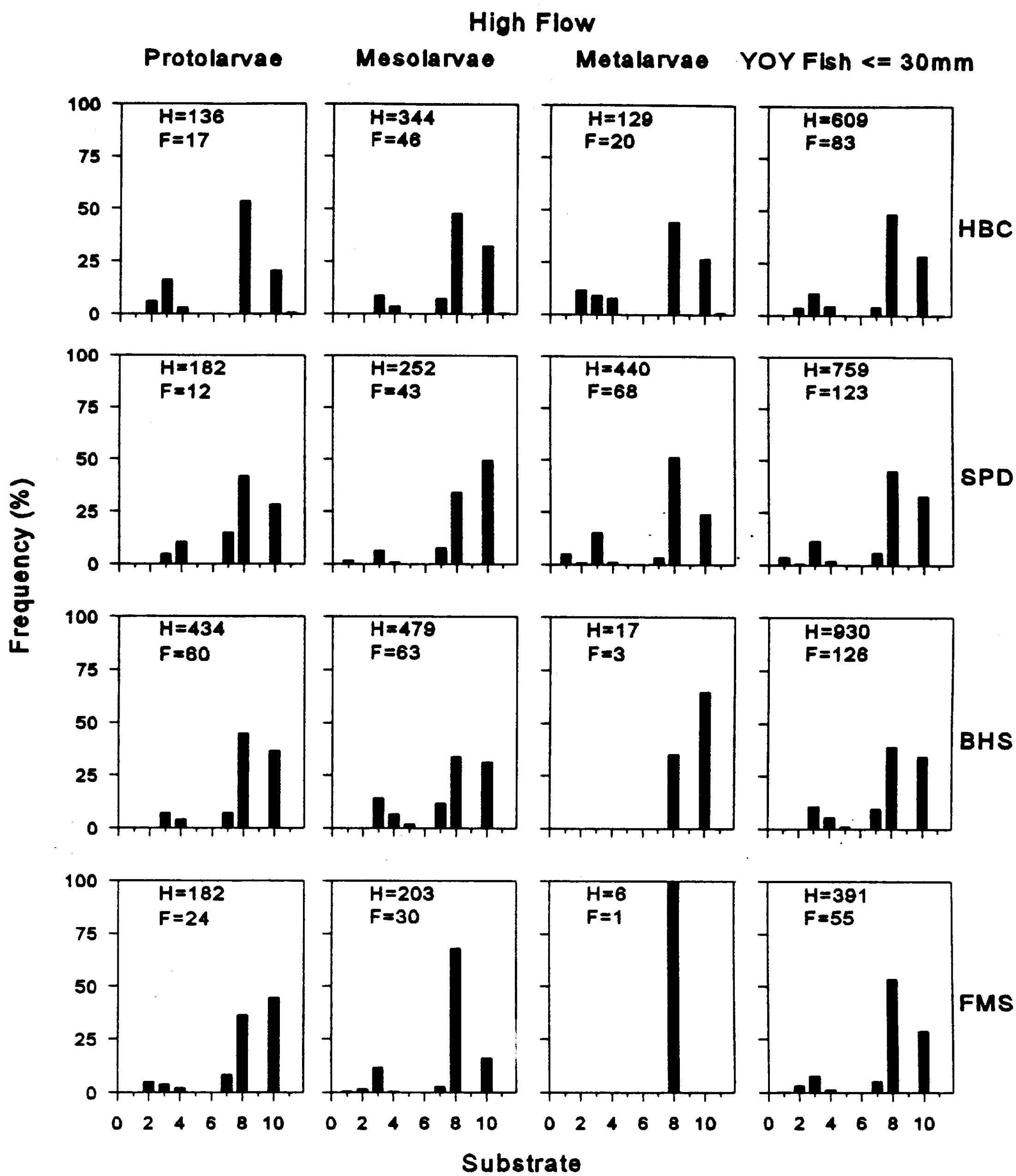
APPENDIX III e. Frequency of "distance from shore" used by larval and YOY fish in LCR near-shore habitats at base flow, 1993. Frequency use of areas > 100 cm from shore is indicated with an asterisk. H = number of habitat points sampled; F = number of fish collected.



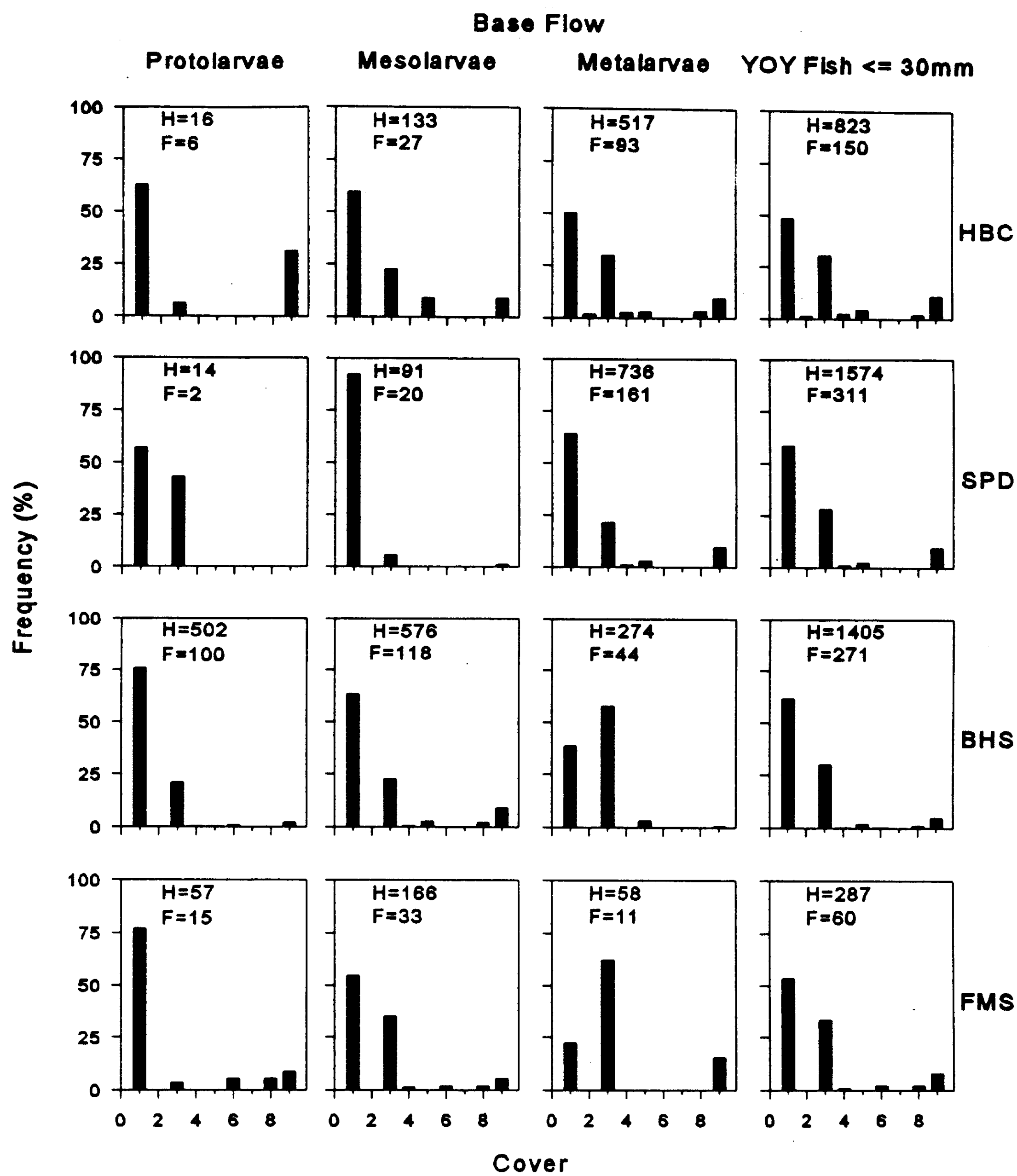
APPENDIX III f. Frequency of "distance from shore" used by larval and YOY fish in LCR near-shore habitats at high flow, 1993. Frequency use of areas > 100 cm from shore is indicated with an asterisk. H = number of habitat points sampled; F = number of fish collected.



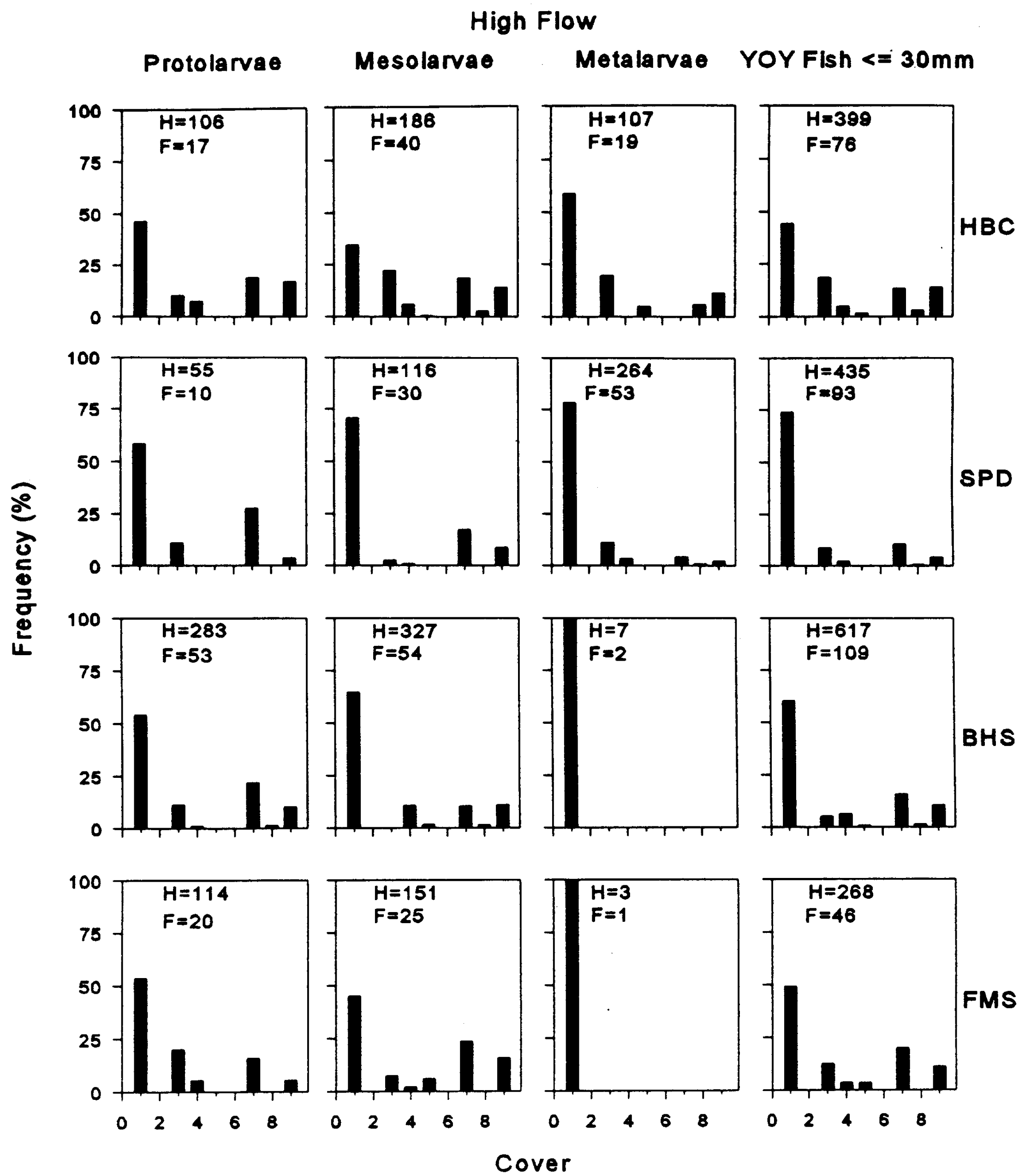
APPENDIX III g. Frequency of substrates (Table 1) used by larval and YOY fish in LCR near-shore habitats at base flow, 1993. H = number of habitat points sampled; F = number of fish collected.



APPENDIX III h. Frequency of substrates (Table 1) used by larval and YOY fish in LCR near-shore habitats at high flow, 1993. H = number of habitat points sampled; F = number of fish collected.



APPENDIX III I. Frequency of cover features (Table 1) used by larval and YOY fish in LCR near-shore habitats at base flow, 1993. H = number of habitat points sampled; F = number of fish collected.



APPENDIX III j. Frequency of cover features (Table 1) used by larval and YOY fish in LCR near-shore habitats at high flow, 1993. H = number of habitat points sampled; F = number of fish collected.